

Received Date : 02-May-2016

Revised Date : 01-Jul-2016

Accepted Date : 22-Jul-2016

Article type : Original Article

**Corresponding Author Email ID:** [tomo.eguchi@noaa.gov](mailto:tomo.eguchi@noaa.gov)

**Predicting overlap between drift gillnet fishing and leatherback turtle habitat in the California Current Ecosystem**

**TOMOHARU EGUCHI<sup>1</sup>, SCOTT R. BENSON<sup>2</sup>, DAVID G. FOLEY<sup>1,3,†</sup>, KARIN A. FORNEY<sup>4</sup>**

1. *Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037*

2. *Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7544 Sandholdt Rd, Moss Landing, CA 95039*

3. *Institute of Marine Sciences, University of California at Santa Cruz, 100 Shaffer Rd, Santa Cruz, CA 95060*

4. *Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 Shaffer Rd, Santa Cruz, CA 95060*

† *Deceased*

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/fog.12181](https://doi.org/10.1111/fog.12181)

This article is protected by copyright. All rights reserved

## **ABSTRACT**

Concern over bycatch of protected species has become a key factor in shaping fisheries management decisions. In 2001, the National Marine Fisheries Service established an annual closure of a large mesh drift gillnet fishery (DGN) targeting swordfish from northern Oregon to central California between August 15 and November 15 due to concerns of bycatch of endangered leatherback turtles (the Pacific Leatherback Conservation Area; PLCA). The spatio-temporal constraints of the PLCA were developed to encompass nearly all previously observed leatherback turtle bycatch events in the fishery. The PLCA has been effective at reducing bycatch of leatherback turtles but has reduced fishing opportunities. In this study, we examine whether the timing of the current PLCA closure is optimal for leatherback turtle conservation, by developing statistical models of leatherback turtle presence inside the PLCA based on environmental variables. We also examine finer-scale spatiotemporal patterns of potential overlap between the fishery and leatherback turtle foraging habitat using Maxent and Random Forests applied to logbook data and leatherback turtle telemetry data. Our results suggest that the temporal extent of the current static closure period is the shortest and most effective for protecting the turtles while allowing fishing during low bycatch-risk periods. We also found that it is possible to predict foraging habitat of leatherback turtles and fishing effort using environmental variables. Identification of spatial and temporal hotspots of potential overlap between fishing effort and leatherback turtle distribution can form a basis for dynamic management approaches.

## **KEY WORDS**

habitat modeling, fishery closure, US west coast, endangered species, bycatch, fishery interactions, swordfish, thresher sharks

## **INTRODUCTION**

Interactions between fishing operations and protected species have been considered a challenging issue throughout the world's oceans (Read *et al.*, 2006; Read, 2008; Wallace *et al.*, 2010). Many international forums and conferences have been convened to discuss bycatch reduction while maintaining fishing operations, e.g., International Fishers Forum

(<http://www.fishersforum.net/>)<sup>1</sup>, American Fisheries Society (<http://www.fisheries.org/>)<sup>2</sup>, and National Marine Fisheries Service (<http://www.nmfs.noaa.gov>). Although gear modifications, time-area closures, and acoustic deterrents have reduced bycatch of some species in particular fisheries (e.g., Gilman *et al.* 2005, 2006, 2008; Larsen *et al.* 2007; Cox *et al.* 2007; Carretta *et al.* 2008), bycatch reduction remains a global management challenge (e.g., Alverson *et al.* 1994; Rivera and Wohl 1999; Eayrs 2007) that is complicated by the lack of a unified international management framework for many fisheries and transboundary species, such as the leatherback turtle (*Dermochelys coriacea*; e.g., Dutton and Squires 2011; Curtis *et al.* 2015; Komoroske and Lewison 2015).

In the U.S., the National Marine Fisheries Service (NMFS) is responsible for sustainably managing diverse marine species, including invertebrates, fishes, marine mammals and turtles, under the Magnuson-Stevens Act (MSA), Marine Mammal Protection Act (MMPA), and Endangered Species Act (ESA). Bycatch is traditionally monitored via observer programs and/or logbooks, and such efforts have been helpful in characterizing fisheries-specific threats and management needs. However, logistical and economic constraints generally limit observer coverage to a fraction of total fishing effort, and logbook records are known to be unreliable (e.g., Read *et al.* 2006; Baker *et al.* 2006; Sampson 2011). Both of these factors contribute to uncertainty in bycatch estimates. Furthermore, for rare species with a low absolute bycatch rate, statistical estimates can be imprecise (Carretta and Moore, 2014). To reduce uncertainty in bycatch estimates, a variety of statistical techniques have been used to correct biases, control for confounding factors, and better understand the temporal and spatial distributions of observed bycatch (Gardner *et al.*, 2008; Sims *et al.*, 2008; Murray, 2009; Murray and Orphanides, 2013; Martin *et al.*, 2015).

While the above tools can help explain observed patterns and reduce uncertainty, different approaches are required to predict bycatch risk to unobserved times or places. Models that consider spatio-temporal variation in fishing behavior as well as the distribution of by-caught species provide the most complete assessment of overlap and potential bycatch risk, because both can be dynamic as ocean conditions change (e.g., Forney 2000; Ferguson *et al.* 2005; Hobday and Hartmann 2006; Forney *et al.* 2011; Block *et al.* 2011). For example, the

---

<sup>1</sup> [http://www.nmfs.noaa.gov/by\\_catch/docs/AFS\\_Bycatch\\_Abstracts.pdf](http://www.nmfs.noaa.gov/by_catch/docs/AFS_Bycatch_Abstracts.pdf).

<sup>2</sup> [http://www.nmfs.noaa.gov/by\\_catch/docs/SeaTurtleTrawlWorkshop.pdf](http://www.nmfs.noaa.gov/by_catch/docs/SeaTurtleTrawlWorkshop.pdf)

distribution of marine predators is affected by the distribution of their prey species, which may in turn be affected by time, static physical features, and dynamic ocean features such as ocean currents, productivity, or water temperature. The distribution of fishing effort may also relate to such environmental cues, as fishermen seek to maximize catch per unit effort based on their knowledge, but other factors such as regulations, fuel and labor costs, the distributions of target species, and the size of fishing vessels also play a role (Soykan *et al.*, 2014).

Telemetry data, when available, can be useful for inferring relationships between species distributions or behavior and environmental conditions or bycatch risk (Jonsen *et al.*, 2003; Morales *et al.*, 2004; Hobday and Hartmann, 2006; Johnson *et al.*, 2008; Seminoff *et al.*, 2008; Benson *et al.*, 2011; Dewar *et al.*, 2011; Shillinger *et al.*, 2011; Zydalis *et al.*, 2011; Roe *et al.*, 2014). Telemetry and fishery data can also provide a basis for developing near real-time management tools to reduce bycatch, e.g., the TurtleWatch products for the Pacific loggerhead (*Caretta caretta*) and leatherback turtles (Howell *et al.*, 2008, 2015). Such dynamic ocean management approaches are increasingly recognized as valuable tools to achieve sustainable fisheries that balance marine resource use and conservation concerns (Lewison *et al.*, 2015; Maxwell *et al.*, 2015). For example, dynamic management might reduce fishing effort or restrict gear types only when species of concern are expected to be present in a specific area of interest. If these species are generally rare, the ability to predict their overlap with fishing activity can be difficult.

In this study, we develop predictive models of fishing effort for the US west coast drift gillnet fishery (the DGN fishery hereafter) and the distribution of endangered leatherback turtles off the U.S. west coast to evaluate the current regulatory measures and evaluate the potential for dynamic management of this fishery in the future. Leatherback turtles are found along the US west coast during summer and autumn, when dense aggregations of jellyfish, especially the brown nettle (*Chrysaora fuscescens*) are common (Graham *et al.*, 2001, 2010; Benson *et al.*, 2007, 2011). Telemetry studies have revealed that these leatherback turtles are part of the Western Pacific nesting population, which has experienced a dramatic (~80%) decline in abundance during the past three decades (Tapilatu *et al.*, 2013).

The DGN fishery targets swordfish (*Xiphias gladius*) and common thresher sharks (*Alopias vulpinus*). The fishery uses a panel of netting suspended vertically in the water, while the net is attached to a vessel at one end and drifts along with the current. Nets are typically set

in the evening, allowed to soak overnight, and retrieved in the morning, where the average soak time is approximately 10 hrs. Although the DGN fishing season is from August 15 to August 14 of the following year, nearly all of the fishing effort occurs from August 15 to January 31 of the following year (NMFS 2013). The DGN fishery is managed federally and requires a permit, which is linked to an individual fisherman. The number of permits has declined from 251 in 1986 to 73 in 2010, with only 16 vessels actively participating in the swordfish gillnet fishery in 2012. Fishing effort has declined from approximately 10,000 annual sets in the mid-1980s to fewer than 500 in recent years, while approximately 15% of all sets have been observed since 1990 (Carretta and Barlow 2011, NMFS unpublished data). There were 25 observed incidental captures of leatherback turtles in the DGN fishery between 1990 and 2014.

To reduce bycatch of leatherback turtles in the DGN fishery (Julian and Beeson, 1998; Carretta *et al.*, 2004), NMFS established the Pacific Leatherback turtle Conservation Area (PLCA, Figure 1) in 2001. The PLCA extends from central Oregon to central California and is closed to DGN fishing annually from August 15 to November 15 (Federal Register 50 CFR Parts 223 and 224). There have been two entanglements of leatherback turtles, both of which were released alive, in the DGN fishery since the PLCA was established (Carretta *et al.* 2014). While this closure has been very effective for reducing leatherback turtle bycatch, it is also restrictive to the fishery, and there may be opportunities for the fishery via dynamic ocean management (Maxwell *et al.*, 2015) given the variable nature of the California Current Ecosystem (Chelton *et al.*, 1982) and variability in leatherback turtle movements and habitat use in this area (Benson *et al.*, 2011).

To examine the feasibility of dynamic management of leatherback turtle bycatch in this fishery, we had two primary objectives. First, we used telemetry data to develop habitat-based predictive models of leatherback turtle presence in the PLCA, which were used to evaluate whether the same level of leatherback turtle protection as the current static closure might be achieved with a closure period based on statistical predictions. Second, we developed spatio-temporal models of inferred leatherback turtle foraging habitat, DGN fishing effort, and their respective overlap at 0.5 degree spatial and 14-day temporal resolutions. This second objective is intended as a feasibility study to examine whether finer-scale dynamic management of the DGN fishery may be possible. We show that the current PLCA closure timing is appropriate, and that co-occurrence of foraging habitat and DGN effort can be predicted at the examined

spatio-temporal scale. These results provide a foundation for future research, such as model-based bycatch simulations, to evaluate potential dynamic management strategies that would increase fishing opportunities while maintaining protection of leatherback turtles and other species.

## **METHODS**

### *Study area*

To investigate the potential overlap between the California DGN fishery and leatherback turtles, we defined our study area to be a polygon bounded by 33.45°N, 46.00°N, 130.00°W and the west coast of the US (Figure 1). This area is part of the California Current Ecosystem (CCE; Mann and Lazier 2006), which is one of the most productive marine ecosystems in the world. The California Current is a southward flowing eastern boundary current that originates in the Gulf of Alaska and flows to the eastern equatorial Pacific. Primary productivity in the ecosystem is largely driven by wind-driven coastal upwelling in spring and summer, which brings nutrient-rich water to the surface followed by periods of relaxation of upwelling and resulting in phytoplankton blooms (Bakun *et al.*, 1974; Lynn and Simpson, 1987). CCE productivity is affected by seasonal, inter-annual, and decadal scale variability. Leatherback turtles are found most often during summer/autumn (July – October) in neritic waters corresponding to the period when upwelling relaxes and sea surface temperature increases, but their abundance and distribution varies interannually (Starbird *et al.*, 1993; Benson *et al.*, 2007, 2011).

### *Data*

#### *Leatherback turtle telemetry data*

The satellite-linked telemetry data in this study were a subset of those used in Benson *et al.* (2011). These tracks had been filtered using the state-space switching model developed by Jonsen *et al.* (2005). We selected those tracks that had positions in our study area, but excluded departure tracks for leatherback turtles that exhibited a flight response immediately after being tagged in nearshore waters of California (Benson *et al.* 2011). A total of 15 individual tracks with 973 location points from 2001 to 2008 were included in this study (Figure 1).

Two datasets were created from the telemetry location data for the two separate objectives of this study. The first dataset was used to predict the timing of leatherback turtle

presence in the PLCA. Telemetry locations were categorized as inside or outside the PLCA (presence and absence, respectively). To consider the possibility that different environmental variables affected entry to and departure from the PLCA, we further separated this dataset into “entry” and “departure” data subsets. Telemetry data indicated that leatherback turtles would enter in the area by August, whereas they would leave the area in late autumn, responding to local oceanographic conditions (Benson et al. 2011). Consequently, the “entry” data subset spanned July 1 through September 30 and the departure subset spanned October 1 to December 31. For all available entrances and departures in the telemetry data, the 30 days before and after were considered as “absences” (Figure 2). Statistical models were fit separately to the entry and departure data subsets.

The second dataset was used to develop a predictive spatial model of inferred leatherback turtle foraging habitat in the PLCA. The PLCA includes portions of two foraging areas that have been designated as critical habitat for leatherback turtles under the ESA (2012; Federal Register 50 CFR Part 226): (1) neritic waters off central California between Point Arena (38.909°N 123.693°W) and Point Arguello (34.577°N 120.647°W) extending offshore to the 3000-m isobath, (2) nearshore waters between Cape Flattery (48.383°N 124.714°W), Washington, and Cape Blanco (42.836°N 124.564°W), Oregon, extending offshore to the 2000-m isobath. Benson et al. (2011) determined a greater probability of foraging in these areas. For the purposes of our feasibility study, we assumed that telemetry positions within either of these critical habitat areas were associated with foraging behavior, whereas those outside of these areas were associated with non-foraging behavior. These data were used to develop models to predict foraging habitat of leatherback turtles using associated environmental variables. We note that leatherback turtles may also be at risk of bycatch when they are not foraging, but habitat associations differ for foraging and non-foraging behavior (Benson et al. 2011). We chose to model foraging habitat as a simple case study to evaluate the potential for spatio-temporal predictions of overlap between leatherback turtles and the DGN fishery. If successful, this would provide a foundation for a more comprehensive bycatch risk analysis that takes into account non-foraging behavior as well.

### The DGN fishery

The DGN dataset used to model fishing effort consisted of the number of sets in 10' × 10' blocks within our study area from 1990 to 2000 (prior to implementation of the PLCA), extracted from logbook records managed by NMFS. Although logbook records are available as far back as 1981, these earlier data could not be included in our model because the availability of environmental variables was limited prior to 1990. The pooled 1990-2000 DGN data form the basis for a predictive model of fishing effort distribution, with the assumption that these data are representative of the underlying mechanisms affecting fishing locations during other years. The model was then used to predict what the distribution of fishing effort might have been during 2001-2010 if the PLCA were not in place, and to examine potential overlap with the 2001-2010 leatherback turtle foraging habitat model.

### Environment

Different environmental variables were used for the two objectives of the study, because the first objective addressed a temporal question (timing of leatherback turtle presence in the PLCA), whereas the second set of models required spatio-temporal habitat information. Temporal variables for the first objective included the upwelling index (UW) at latitudes 36°N, 39°N, 45°N and 48°N (Bakun, 1973; Schwing and Mendelssohn, 1997; Bograd *et al.*, 2009), the Northern Oscillation Index (NOI; Schwing *et al.* 2002), the Pacific Decadal Oscillation Index (PDO; Mantua *et al.* 1997) and the day of the year (DOY). UW and NOI were obtained from the NOAA Fisheries, Environmental Research Division<sup>3</sup>, whereas PDO was obtained from the Joint Institute for the Study of Atmosphere and Ocean<sup>4</sup>. Possible cumulative effects or time lags over time were considered by extracting the indices over 30, 60, and 90 days prior to each telemetry data point and computing the mean, standard deviation (s), and cumulative (cumu) values. Variables were defined as follows; abbreviated variable name, latitude, statistic, and lag period. For example, UW36s\_60d indicates the standard deviation of UW index at 36N over 60 days.

For the second objective, i.e., to predict the distributions of leatherback turtle foraging habitat and the DGN fishery, nine spatio-temporal environmental variables were selected based

---

<sup>3</sup> <http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/>

<sup>4</sup> <http://research.jisao.washington.edu/pdo/PDO.latest>



on the results of Benson et al. (2011); primary productivity (PP), sea surface temperature (SST), total kinetic energy (TKE), wind-driven upwelling (WEKM), sea surface height (SSH), sea surface height variability (SSHV), sea surface height anomaly (SSHA), and meridional and zonal geostrophic current speed (UGEO and VGEO, respectively). These data were acquired from the data access website of NOAA Fisheries, Environmental Research Division<sup>5</sup> using Matlab (MathWorks, Inc.) routines available from the same website. All variables were acquired at their native resolutions but aggregated to match our prediction resolution of 0.5×0.5 degree polygons. Primary productivity data ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) were 8-day composites (MODIS; Figure 3). SST data ( $^{\circ}\text{C}$ ) were 8-day composites from two different sources (AVHRR and MODIS/GOES/AVHRR) available for two different periods (Figure 3). Geostrophic current data ( $\text{m s}^{-1}$ ) in meridional (U) and zonal (V) directions were obtained from altimetry sensors on various satellites. TKE was computed as  $\frac{1}{2}(U^2 + V^2)$  (Ducet *et al.*, 2000). WEKM is a measure of wind-driven upwelling from wind stress (Xie and Hsieh 1995). SSH (m) were obtained from altimetry sensors aboard multiple satellites (Table 1). SSHV is the root mean square in SSH within each cell ( $0.5 \times 0.5$  degrees) and SSHA is the difference between the observed SSH and the long-term average. For the 1990-2000 DGN fishery, we used static variables (latitude, longitude, depth, and day of year) combined with sea surface temperature (SST) as the only dynamic variable because fewer dynamic variables were available (Figure 3). Depths (m) were obtained from the NOAA National Geophysical Data Center website<sup>6</sup>. We also considered possible effects of time lag (8, 14, or 30 days) between oceanographic variables and turtle/fishery habitat; for example, the 8-day lagged data for the second half of August 1995 (August 15-31) would consist of environmental data from August 7 to August 23, 1995.

Throughout this manuscript, spatial environmental variables are abbreviated in the following manner: abbreviated variable name (e.g., SSH) followed by statistic, then time lag. For example, SSHs\_30d would indicate the standard deviation of sea surface height over 30 days.

---

<sup>5</sup> <http://coastwatch.pfeg.noaa.gov/erddap/index.html>

<sup>6</sup> <http://www.ngdc.noaa.gov>

### *Predictive models*

Different analytical tools were used for the three different predictive models (presence of leatherback turtles in the PLCA, foraging habitat of leatherback turtles, and DGN fishing locations), because of differences in the available data and their statistical properties. Each will be described separately below.

#### *Presence of leatherback turtles in the PLCA*

The temporal presence and absence of leatherback turtles in the PLCA was modeled using a mixed effects logistic regression framework. First, however, we determined the variables that were useful in modeling presence/absence of leatherback turtles in the PLCA for entry and departure separately using a conditional Random Forests (RF) classification approach (*cforest* in R package *party*; Hothorn *et al.* 2006; Strobl *et al.* 2007, 2008) in the R statistical environment. Because specific locations were not used in this analysis (i.e., we examined only whether or not a particular telemetered location was inside of the PLCA), data were treated as a binary response. The performance of the RF model was evaluated using the confusion matrix (R package *caret*; Max *et al.* 2013) on out-of-bag predictions, which were the predictions for data points that were not used to build models. To evaluate the prediction accuracy, we used the kappa statistic ( $\kappa$ ; Cohen 1960), which measured the proportional increase in predicted accuracy relative to an expected accuracy. Higher values indicated better predictive performance.

In the RF approach, variable importance can be determined by two measures; (1) how prediction error changes when a variable is randomly permuted (Breiman, 2001) and (2) how AUC (area under the receiver operator characteristics curve) changes when a variable is randomly permuted (Janitza *et al.*, 2013). In addition to these variable importance measures, we added a random number variable, which consisted of random numbers from a uniform distribution between 0 and 100. Variables that were less useful in predicting the presence/absence of leatherback turtles in the PLCA than random numbers were discarded.

Using the variables identified as important by the RF analysis, we developed mixed-effects linear logistic regression models on presence/absence data, where individuals were treated as the random effect variable. The RF approach was not affected by correlations among predictor variables (Breiman, 2001), but the regression approach would have been affected. Consequently, pair-wise correlations were computed among the predictor variables and

candidate logistic regression models were only allowed to include uncorrelated variables. Models were fitted to the data using a Bayesian approach (Bayesian linear mixed effects models; BLMM) using the *rjags* package (Plummer 2015). Convergence was determined using the Gelman-Rubin statistic (Gelman et al. 2015). The models were compared using approximate Deviance Information Criteria (DIC; Gelman et al. 2015).

The selected models for entry and departure then were used to predict the median daily probability of presence of leatherback turtles in the PLCA when the DGN fishery was operating in the area, 1990 to 1999. For each of these years, probabilities of turtle presence in the PLCA were computed for July 1 (DOY = 182) to September 30 (September 29 for the leap years; DOY = 273) using the entry dataset, for October 1 (September 30 for the leap years) to December 31<sup>st</sup> using the departure dataset, and the medians of the posterior distributions.

#### Foraging habitat of leatherback turtles

To predict foraging habitat of leatherback turtles in the study area, we used an RF approach because it allowed us to mine our data without the need to eliminate correlated predictor variables (Breiman, 2001). Telemetry locations within the critical habitat areas (Fig. 1) were considered to be 'foraging' and locations outside these areas were considered non-foraging. Analyses were performed using the *cforest* function in the *party* package (Hothorn *et al.*, 2006; Strobl *et al.*, 2007, 2008) in the R statistical environment. Although RF are not prone to overfitting and predictive power is increased by including as many variables as possible (Breiman, 2001; Hothorn *et al.*, 2006; Strobl *et al.*, 2007, 2008), we strived to build parsimonious models. Therefore, useful variables for predicting foraging habitat were selected using the same variable selection process described above. Model predictions of leatherback turtle habitat were then made for the years 2001-2010 at a  $0.5 \times 0.5$  degree spatial resolution and 14-day temporal resolution.

#### DGN fishing locations

The DGN fishery prediction required a different approach (Maxent; Phillips et al. 2006, Phillips & Dudik 2008) because logbook data only provide presence locations. Ideally, Maxent analyses should encompass the full range of environmental conditions (background) available to the fishery and sample the background with a similar bias as the presence points (Phillips *et al.*,

2009; Elith *et al.*, 2011). Because we did not have a means to sample background data as fishers selected their set locations, we selected the background environmental data systematically from a grid. The spatial distribution of DGN fishing was modeled as a function of latitude, longitude, day of the year (DOY), depth, and SST with possible effects of time lag (8, 14, and 30 days). As for the leatherback turtle data, we used random numbers to evaluate usefulness of environmental variables for predictions. After determining variables that were more useful than random numbers, models were rebuilt using only those variables.

Maxent modeling requires a few parameters to be set, including prevalence, regularization parameter, and features. The prevalence parameter ranges from 0 to 1 and represents the probability of presence given the environment (Elith *et al.*, 2011). Therefore, in general, the parameter should be set according to the abundance of the species; larger values for abundant species and vice versa. The particular value of prevalence becomes important when multiple species of various abundances are compared in predicted probabilities of occurrence using the Maxent approach (Elith *et al.*, 2011). The default value of 0.5, however, is often used when abundance information is lacking. Because we pooled data for all years and we were not comparing among multiple species, we used the default value of 0.5. The regularization parameter in Maxent penalizes complex models but there is no particular value that can be used for all analyses. It has been recommended that a user needs to explore different values of the regularization parameter. Smaller values fit the data well but may have less applicability to new data. Following the advice in Phillips & Dudík (2008), we tested various values of the regularization parameter (0.05, 0.1, 0.22, 0.46, and automatic selection). Only two of the available features in the Maxent package (linear, quadratic, polynomial, hinge, and threshold), were allowed in each model for simplicity and interpretability. Among all possible combinations, we considered the following six: linear + quadratic (LQ), linear + polynomial (LP), linear + threshold (LT), hinge + quadratic (HQ), quadratic + threshold (QT), and hinge + threshold (HT).

To compare the performance of models, four-fold cross validations were used to develop models on  $\frac{3}{4}$  of the total dataset (training data) and to test the fit on the remainder (test data). All combinations (30) of five regularization parameters and six features were compared using three statistics on test data; gain, AUC, and prediction power. Gain in Maxent is the average log probability of the presence samples, therefore, gain, or  $\exp(\text{gain})$  to be exact, provides a metric

of how much greater the average likelihood was at the presence datum compared with a random background point (Phillips *et al.*, 2006). The AUC in the Maxent modeling approach is interpreted as the probability that a randomly selected presence data point is ranked above a random background site (Phillips *et al.* 2006). Finally, we used a confusion matrix, especially the probability of correctly predicting presence of DGN fishing in the test data (sensitivity), as the third measure of model performance.

In addition to these statistics, we used response curves of explanatory variables to select feature combinations that were not overly complicated. In other words, feature combinations with response curves with many “wiggles” were avoided even if the model selection statistics (gain, sensitivity, and AUC) indicated good fits. The best combination of a model and a set of variables through this process was used for predictions of the relative DGN fishing likelihood of the  $0.5 \times 0.5$  degree polygons over 2-week periods in the years without fishing data, *i.e.*, after 2000. All Maxent analyses were conducted using Maxent software (v. 3.3.3k; Phillips *et al.* 2006) through the *dismo* package (v. 1.0.5, Hijman *et al.* 2014) in the R statistical environment.

#### Co-occurrence of leatherback turtles and DGN fishing

To predict the co-occurrence of leatherback turtle habitat and the DGN fishery, we predicted turtle habitat and fishing effort distribution on the same temporal (14-day periods between August 15 and November 15 from 2001 to 2010) and spatial scales ( $0.5 \times 0.5$  degree polygon). We then averaged over the 10-year period to create average co-occurrence likelihoods for each 14-day period. It is important to note that a high likelihood of leatherback turtle habitat (or DGN fishing location) does not equate to a high density of turtles (or DGN presence), because it is affected by the abundance of turtles (or DGN fishing vessels) in the area. As an extreme example, if there were one leatherback turtle (or DGN fishing vessel) in the area, even if there were many areas of predicted foraging (or fishing) habitat, no more than one can be occupied by the turtle (or the fisher) at any given time. Nonetheless, the product of the likelihoods of leatherback habitat and fishing activity within each  $0.5 \times 0.5$  degree polygon provides a relative measure of bycatch risk, because the two processes are independent from one another.

## RESULTS

### *Presence of leatherback turtles in the PLCA (logistic regression)*

#### Entry to the PLCA

According to the RF variable importance measures, the most influential variables for the prediction of entry to the PLCA by leatherback turtles were standard deviation (s) and cumulative sum (cumu) of upwelling indices (UW) at 36 and 39 °N (UW36s\_90d, UW36s\_60d, UW36cumu, and UW39cumu, where 60d and 90d refer to time lags of 60 and 90 days respectively). The RF model accurately predicted the presence/absence of leatherback turtles in the PLCA, yielding 87% of correct assignments and a  $\kappa$  statistic of 0.71. High pair-wise correlations were found between UW36cumu and UW39cumu (Pearson correlation = 0.96) and between UW36s\_60d and UW36s\_90d (Pearson correlation = 0.85). Therefore, using the only uncorrelated variables, four candidate models were developed, where Model 4 (UW36s\_60d + UW39cumu) was identified as the best based on DIC values (Table 3). Convergence of Markov chains for all models was confirmed via the Gelman-Rubin statistic ( $< 1.01$ ). The estimated coefficients indicated that the likelihood of leatherback turtles entering the PLCA was high when the standard deviation of the UW index over 60 days at 36N (UW36s\_60d) is small (negative coefficient) and cumulative UW index at 39N (UW39cumu) is high (positive coefficient; Table 3). The estimated standard deviation for the random effects, i.e., individual-level variability, was 31.2 (95%PI = 19.2-53.9; Table 3).

#### Departure from the PLCA

The order of important variables for the departure dataset was different from that for the entry dataset. Various statistics for the upwelling index at 48° N were determined to be important. The prediction of departure from the PLCA using RF was accurate, yielding 96% of correct assignments and a  $\kappa$  statistic of 0.92. Pair-wise correlations of the six most important variables indicated that the top five variables were strongly correlated to each other. Consequently, we used the mean upwelling index at 48N over 60 days (UW48mean\_60d) and PDO to develop four candidate logistic regression models including an interaction between the two (Table 4). The DIC values indicated that Model 3, with both variables, was better than Model 4, which included an interaction between the two variables. PDO had a negative effect whereas UW48mean\_60d had a positive effect on the probability of leatherback turtles' presence

in the PLCA. In other words, leatherback turtles departed the PLCA when the mean UW index over 60 days at 48° N (UW48mean\_60d) was low and PDO was high. The estimated standard deviation for the random effects, i.e., individual-level variability, was 9.12 (95%PI = 5.22-18.11), which was smaller than the same parameter for the entry dataset (31.2, 95%PI = 19.2 – 53.9; Table 3).

Based on the combined entry and departure models, the median probability of leatherback turtle presence in the PLCA increased rapidly during mid-July, which was earlier than the beginning of the existing fishery closure (August 15; Figure 4). The probability decreased in November and December in the 10 year period from 1990 to 1999.

#### *Foraging habitat of leatherback turtles (Random Forest)*

Among the environmental variables used in the analysis (i.e., SST, UGEO, VGEO, WEKM, PP, SSH, SSHV, SSHA, TKE, and DOY), all variables with various time lags were more important than random numbers. Although primary productivity (PP) appeared to be an influential variable, PP was not available at many times and locations because of cloud cover. Therefore, we selected an alternate model that included SST, SSH, and SSHV at various time lags and had the same predictive accuracy as the model including PP (0.96 for both). The selected RF model correctly predicted 98% (585/599) of the non-foraging habitat and 91% (269/294) of the foraging habitat, as defined in this study. Predictions were qualitatively consistent with known leatherback turtle foraging habitat (Supplemental Figure 1, Benson et al. 2011).

#### *DGN fishing locations (Maxent)*

Based on a comparison of the three statistics used to evaluate the Maxent predictions (AUC, gain, and sensitivity) and response curves, we selected a model with hinge and quadratic features (HQ), using all variables, and a regularization parameter value of 0.1 as the best performing model. This model had an AUC value for the test data of 0.84 (the probability that a randomly selected presence point was ranked higher than a randomly selected background point),  $\exp(\text{gain})$  without the random number variable of 2.35 (how much greater the average likelihood was at the presence point compared with a random background point), and sensitivity of 0.63 (the probability of correctly predicting presence of DGN fishing in the test data).

For both variable selection statistics (contribution and importance), SST lagged by 30 days (SST30) and latitude were the two most important variables. Among the six most useful variables (i.e., SST30, SST14, SST0, Depth, Longitude, Latitude), SST14 appeared to have the most useful information by itself (the highest training gain) whereas latitude appeared to have the most information that is absent in the other variables (decreased the gain the most when it was omitted). The response curve for SST30 indicated that likelihood of a DGN set increased with 30-days lagged SST, especially above 16 °C. The predicted DGN fishery for 2001-2010 indicated relatively high likelihood of fishing nearshore, perhaps moving southward in summer and fall months (Supplemental Figure 2).

#### *Co-occurrence of leatherback turtle foraging habitat and DGN fishing*

The maximum likelihood of co-occurrence of leatherback turtle foraging habitat and DGN fishing gear within the study area was generally highest during September/October and lowest during November (Figure 6). The variability among years was greatest during the first half of September. The variability decreased during October and November. The mean co-occurrence likelihood for the 2001-2010 period indicated that high likelihood of co-occurrence was found in nearshore areas of central California during September and October (Figure 6). Offshore areas, on the other hand, exhibited low co-occurrence likelihood mostly due to the low likelihood of turtle foraging habitat.

## **DISCUSSION**

#### *Presence of leatherback turtles in the PLCA*

Different sets of environmental variables affected entry to and departure from the PLCA by leatherback turtles. Likelihood of entry to PLCA by leatherback turtles increased as the season progressed in early summer and with increasing cumulative UW index at 39N. The likelihood of entry, however, decreased with increasing variability of the UW index at 36N over 60 days. This is consistent with our understanding of leatherback turtle behavior, where strong and consistent upwelling in the spring followed by relaxation of upwelling is necessary to create favorable conditions for the turtles (Benson et al. 2007, 2011).

In contrast, departure from the PLCA was linked to various statistics of the upwelling index at higher latitude (48N) than for entry (36N and 39N). As the upwelling index at 48N



decreased, the probability of departure increased (or probability of presence decreased). This result might be caused by the three tracks in the northern part of the study area. The RF analysis without these tracks resulted in the upwelling index at 39N to be important (results not shown). A larger sample size will be necessary to tease out the effects of spatial variability of tracks within the study area. Overall, the model predictions fit well with our understanding of the timing of leatherback turtle occurrence in the PLCA. Probability of leatherback turtle occurrence increased in mid-July, prior to the current mid-August PLCA closure period. The probability decreased in the mid November broadly coinciding with the current closure (Figure 4).

The current time-area closure for the DGN fishery along the west coast of the US seems to be effective. Had the fixed time-area closure regulation existed in the 1990s, 18 of 19 observed bycatch events between August 15 and November 15 could have been avoided. In this study, we developed a statistical approach to model the presence of leatherback turtles in the PLCA. For example, the DGN fishery might be restricted in the PLCA when the probability of leatherback turtle occurrence is greater than some threshold value. This could result in an annual fishery closure period that is longer or shorter than the current fixed closure design. Using probability thresholds of 0.5, 0.6, or 0.7 to dynamically close the fishery would have avoided 18 of the observed bycatch events (the same as the existing closure), although specifics differed for two years. Four additional bycatch events would have occurred (1 in 1991 and 3 in 1992) if the above probability approach had been used instead of the existing PLCA closure (Figure 4). The probabilistic approach would not, however, have shortened the closure duration. Further, there is inherent uncertainty in probabilistic predictions for any given year, although the posterior distributions of the coefficients could be used to assess uncertainty explicitly. Overall, the results of our model of leatherback presence in the PLCA suggest that the current August 15 – November 15 closure is the shortest and most effective for protecting leatherback turtles in the PLCA while allowing fishing during low-risk bycatch periods.

#### *Co-occurrence of leatherback turtles and DGN fishing*

We found that telemetry data and the RF approach can be used to predict foraging habitat of leatherback turtles throughout the entire PLCA when some foraging areas in this region are known *a priori*. Known foraging habitats along the coast were predicted to be good foraging habitat even though spatial reference variables (latitude and longitude) were not included in the

predictive model (Figure 6). Areas identified as foraging habitat in this study correspond well to areas where foraging was inferred from telemetry studies, in which a different approach was used (Benson et al. 2011). DGN fishing effort predictions using Maxent appeared less precise, possibly because only one dynamic variable, SST, was available. The response curve for SST30 indicated that fishing occurred in a narrow SST band, especially lagged by 30 days. Fishers may be cueing in on certain SST values based on their experience with their target catch (swordfish and thresher sharks). Additional environmental variables might increase the precision of these models, and recent advances in data-assimilative ocean circulation models (e.g., Moore *et al.* 2011) may allow the use of ocean-model based habitat predictors, which have shown promise for predicting cetacean distributions in the California Current ecosystem (Becker *et al.*, 2016). Economic and logistic factors are also likely to play a role in the distribution of fishing effort, potentially masking environmental patterns (Soykan *et al.*, 2014).

Although there is uncertainty in both of the above models and they were developed from data sets spanning different time periods, the combined model of potential overlap between leatherback foraging habitat and fishing effort provides a starting point for evaluating finer-scale spatiotemporal patterns of potential bycatch risk to leatherback turtles within our study area. Months with lower documented bycatch rates (August and November) were also predicted to have low overlap in our combined model. Further, most of the actual bycatch events observed during 1990-2000 were located in areas of greater predicted overlap (Figure 6). In particular, overlap was predicted to be high during late September and October off central California, where and when the majority of observed leatherback bycatch events took place. However, we emphasize that this analysis only considers overlap between foraging habitat of leatherback turtles and the DGN fishery. The late October and November bycatch events that are in areas of low predicted overlap suggest that bycatch also occurs when turtles left nearshore foraging areas and were transiting through DGN fishing areas.

The ability of our models to capture at least some of the documented bycatch patterns suggests that there may be options for dynamic management of the DGN fishery in the future. However, more comprehensive models that include both foraging and transiting behavior of leatherback turtles, coupled with simulation analyses to address model uncertainties, will be required to allow the evaluation of potential dynamic management strategies. Model-based predictions should also be validated with independent data sets, such as surveys of fishing gear

locations (or through vessel monitoring system) and leatherback turtles. These additional analyses may require new data sets that include systematic information on both presence and absence of turtles and fishing effort.

Fishery independent survey data on the distribution of by-caught species, such as sea turtles, have been shown to be useful in understanding fishery bycatch, especially when combined with fishery dependent data (Murray and Orphanides, 2013). Design-based studies, e.g., aerial line-transect surveys conducted over large areas and sufficiently long time periods, are essential to capture interannual and seasonal variability in leatherback turtle distributions. Telemetry data can also provide information on leatherback turtle movements and inferred behavior (e.g. Benson et al. 2011, Shillinger et al. 2011). Additional other presence/absence data can provide more precise predictions of species distribution based on environment and allow estimation of densities (Aarts et al. 2008).

Similarly, fishery logbooks only provide presence data, because there is no record of areas that the vessel passed through without making a set. True absence data should be collected whenever possible (Phillips *et al.*, 2009; Wisz and Guisan, 2009; Aarts *et al.*, 2012), for example, by obtaining tracks of fishing vessels to provide information on locations where fishers could have set their gear but did not. If this is not possible, an alternate approach is the creation of pseudo-absence points (e.g., Guisan *et al.* 2002; Stokland *et al.* 2011; Zydalis *et al.* 2011; Barbet-Massin *et al.* 2012), but care must be taken when generating pseudo-absences, as this can affect the accuracy of Maxent predictions (Phillips *et al.*, 2009; VanDerWal *et al.*, 2009).

The results of our study provide a foundation for future explorations of dynamic ocean management scenarios for the DGN fishery that would protect leatherback turtles and other species. However, our results suggest that such a dynamic management framework will need to be dynamic in both space and time, which requires more precise and comprehensive models of leatherback turtle behavior and fishing effort distributions than possible with the currently available data. This is likely caused, in part, by the highly variable nature of the California Current Ecosystem, compared to, for example, the central North Pacific, where simple models of sea turtle and fishery overlap were developed to estimate near-real time bycatch risk within the fishing area (Howell *et al.*, 2008, 2015).

The collection of adequate new data to improve predictive models of leatherback turtles and the DGN fishery will likely require multiple years of dedicated research. Therefore,

alternative tools for allowing swordfish fishing within the California Current Ecosystem while minimizing bycatch risk should continue to be explored. Changes in hook and bait types have reduced loggerhead and leatherback turtle bycatch in Hawaii-based longline fisheries while retaining or increasing the target species catch rate (Gilman *et al.*, 2007). Studies of the vertical and horizontal distributions of target species (e.g., Abecassis *et al.* 2012; Sepulveda *et al.* 2014) and protected species may allow the development of alternate gear types to maximize exposure to target species and minimize risk to protected species. For example, the bycatch of air-breathing species such as sea turtles and marine mammals potentially can be reduced if fishing gear is deployed deeper within the water column. Recent studies on deep-set buoy gear targeting swordfish show promise if catch rates can become economically viable (Sepulveda *et al.*, 2014).

In conclusion, the results of our study indicate that the current PLCA closure period is effective for reducing leatherback turtle bycatch in the DGN fishery. Model predictions confirmed that the current PLCA eliminates most of the spatial and temporal bycatch risk to leatherback turtles. With additional data, finer-scale dynamic refinements to this closure are possible, but the challenges of implementing and enforcing such dynamic management are complex, given the temporal and spatial scales that vessel captains base their fishing decisions upon. Additional data and expanded modeling studies will be required to develop and test potential dynamic management scenarios.

## **ACKNOWLEDGMENTS**

Satellite telemetry transmitters were deployed on leatherback turtles were conducted under Endangered Species Act permit numbers 1159, 1227, and 1596 using approved animal handling protocols and in conformance with all applicable laws. We thank the data managers at Fisheries Resources Division of the Southwest Fisheries Science Center for converting DGN fishery logbook data into an electronic format and making them available. We appreciate Jeffrey Seminoff, Jim Carretta, and anonymous reviewers for providing constructive comments, which improved the manuscript. The authors acknowledge that there is no conflict of interest to declare.

## **REFERENCES**

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., and Matthiopoulos, J. (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* **31**:140-160.

- Aarts, G., Fieberg, J., and Matthiopoulos, J. (2012) Comparative interpretation of count, presence-absence and point methods for species distribution models. *Methods Ecol. Evol.* **3**: 177–187.
- Abecassis, M., Dewar, H., Hawn, D., and Polovina, J. (2012) Modeling swordfish daytime vertical habitat in the North Pacific Ocean from pop-up archival tags. *Mar. Ecol. Prog. Ser.* **452**: 219–236.
- Alverson, D.L., Freeberg, M.H., Pope, J.G., Murawski, S.A. (1994). A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper 339: 233 pp. Available from: <http://www.fao.org/DOCREP/003/T4890E/T4890E00.HTM#TOC>
- Baker, C.S., Lukoschek, V., Lavery, S., Dalebout, M.L., Yong-un, M., Endo, T., and Funahashi, N. (2006) Incomplete reporting of whale, dolphin and porpoise “bycatch” revealed by molecular monitoring of Korean markets. *Anim. Conserv.* **9**: 474–482.
- Bakun, A. (1973) Coastal upwelling indices, West coast of North America 1946-1971. *NOAA Tech. Rep. NMFS* **671**: pp. 112.
- Bakun, A., McLain, D.R., and Mayo, F. (1974) Mean annual cycle of coastal upwelling off western North America as observed from surface measurements. *Fish. Bull.* **72**: 843–844.
- Barbet-Massin, M., Jiguet, F., Albert, C.H., and Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: How, where and how many? *Methods Ecol. Evol.* **3**: 327–338.
- Becker, E., Forney, K., Fiedler, P., Barlow, J., Chivers, S., Edwards, C., et al. (2016) Moving towards dynamic ocean management: How well do modeled ocean products predict species distributions? *Remote Sens.* **8**: 149.
- Benson, S.R., Eguchi, T., Foley, D.G., Forney, K.A., Bailey, H., Hitipeuw, C., et al. (2011) Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. *Ecosphere* **2**: Article 84.
- Benson, S.R., Forney, K.A., Harvey, J.T., Carretta, J. V, and Dutton, P.H. (2007) Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990–2003. *Fish. Bull.* **105**: 337–347.
- Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., et al. (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**: 86–90.

- Bograd, S.J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W.J., and Schwing, F.B. (2009) Phenology of coastal upwelling in the California Current. *Geophys. Res. Lett.* **36**: 1–5.
- Breiman, L. (2001) Random Forests. *Mach. Learn.* **45**: 5–32.
- Carretta, J. V. and Barlow, J. (2011) Long-term effectiveness, failure rates, and “dinner bell” properties of acoustic pingers in a gillnet fishery. *Mar. Technol. Soc. J.* **45**: 7–19.
- Carretta, J. V., Barlow, J., and Enriquez, L. (2008) Acoustic pingers eliminate beaked whale bycatch in a gill net fishery. *Mar. Mammal Sci.* **24**: 956–961.
- Carretta, J. V., Enriquez, L., and Villafna, C. (2014) Marine mammal, sea turtle, and seabird bycatch in California gillnet fisheries in 2012. *NOAA Tech. Memo. SWFSC* **526**: 20 pp.
- Carretta, J. V. and Moore, J.E. (2014) Recommendations for pooling annual bycatch estimates when events are rare. *NOAA Tech. Memo. SWFSC* **528**: 11 pp.
- Carretta, J. V., Price, T., Petersen, D., and Read, R. (2004) Estimates of marine mammal, sea turtle, and seabird mortality in the California drift gillnet fishery for swordfish and thresher shark, 1996 – 2002. *Mar. Fish. Rev.* **66**: 21–30.
- Chelton, D., Bernal, P., and McGowan, J. (1982) Large-scale interannual physical and biological interaction in the California current. *J. Mar. Res.* **40**: 1095–1125.
- Cohen, J. (1960) A coefficient of agreement of nominal scales. *Educ. Psychol. Meas.* **20**: 37–46.
- Cox, T.M., Lewison, R.L., Zydalis, R., Crowder, L.B., Safina, C., and Read, A.J. (2007) Comparing effectiveness of experimental and implemented bycatch reduction measures: the ideal and the real. *Conserv. Biol.* **21**: 1155–64.
- Curtis, K.A., Moore, J.E., and Benson, S.R. (2015) Estimating limit reference points for western Pacific leatherback turtles (*Dermochelys coriacea*) in the U.S. west coast EEZ. *PLoS One* **10**: e0136452.
- Dewar, H., Prince, E.D., Musyl, M.K., Brill, R.W., Sepulveda, C., Luo, J., et al. (2011) Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *Fish. Oceanogr.* **20**: 219–241.
- Ducet, N., Le Traon, P.Y., and Reverdin, G. (2000) Global high-resolution mapping of ocean circulation from TOPEX/Poseidon and ERS-1 and -2. *J. Geophys. Res.* **105**: 19477–19498.
- Dutton, P.H. and Squires, D. (2011) A holistic strategy for Pacific sea turtle conservation. Pages 37-59 in P.H. Dutton, D. Squires, A. Mahfuzuddin (eds). Conservation and sustainable

management of sea turtles in the Pacific Ocean. University of Hawaii Press, Honolulu, Hawaii, USA.

- Eayrs, S. (2007) A guide to bycatch reduction in tropical shrimp-trawl fisheries. Revised Edition. Rome, FAO, 2007. 108 pp. Available from:  
<ftp://ftp.fao.org/FI/DOCUMENT/rebyc/a1008e.pdf>
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., and Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **17**: 43–57.
- Ferguson, M.C., Barlow, J., Reilly, S.B., and Gerrodette, T. (2005) Predicting Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale population density from habitat characteristics in the eastern tropical Pacific Ocean. *J. Cetacean Res. Manag.* **7**: 287–299.
- Forney, K.A. (2000) Environmental models of cetaceans abundance: Reducing uncertainty in population trends. *Conserv. Biol.* **14**: 1271–1286.
- Forney, K.A., Kobayashi, D.R., Johnston, D.W., Marchetti, J.A., and Marsik, M.G. (2011) What's the catch? Patterns of cetacean bycatch and depredation in Hawaii-based pelagic longline fisheries. *Mar. Ecol.* **32**: 380–391.
- Gardner, B., Sullivan, P., Epperly, S., and Morreale, S. (2008) Hierarchical modeling of bycatch rates of sea turtles in the western North Atlantic. *Endanger. Species Res.* **5**: 279–289.
- Gilman, E., Brothers, N., and Kobayashi, D.R. (2005) Principles and approaches to abate seabird by-catch in longline fisheries. *Fish Fish.* **6**: 35–49.
- Gilman, E., Kobayashi, D., and Chaloupka, M. (2008) Reducing seabird bycatch in the Hawaii longline tuna fishery. *Endanger. Species Res.* **5**: 309–323.
- Gilman, E., Kobayashi, D., Swenarton, T., Brothers, N., Dalzell, P., and Kinankelly, I. (2007) Reducing sea turtle interactions in the Hawaii-based longline swordfish fishery. *Biol. Conserv.* **139**: 19–28.
- Gilman, E., Zollett, E., Beverly, S., Nakano, H., Davis, K., Shiode, D., et al. (2006) Reducing sea turtle by-catch in pelagic longline fisheries. *7*: 2–23.
- Graham, T.R., Harvey, J.T., Benson, S.R., Renfree, J.S., and Demer, D.A. (2010) The acoustic identification and enumeration of scyphozoan jellyfish, prey for leatherback sea turtles (*Dermochelys coriacea*), off central California. *ICES J. Mar. Sci.* **67**: 1739–1748.
- Graham, W.M., Pagès, F., and Hamner, W.M. (2001) A physical context for gelatinous zooplankton aggregations: A review. *Hydrobiologia* **451**: 199–212.

- Guisan, A., Edwards, T.C., and Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Modell.* **157**: 89–100.
- Hobday, A.J. and Hartmann, K. (2006) Near real-time spatial management based on habitat predictions for a longline bycatch species. *Fish. Manag. Ecol.* **13**: 365–380.
- Hothorn, T., Hornik, K., and Zeileis, A. (2006) Unbiased recursive partitioning: A conditional inference framework. *J. Comput. Graph. Stat.* **15**: 651–674.
- Howell, E.A., Hoover, A., Benson, S.R., Bailey, H., Polovina, J.J., Seminoff, J.A., and Dutton, P.H. (2015) Enhancing the TurtleWatch product for leatherback sea turtles, a dynamic habitat model for ecosystem-based management. *Fish. Oceanogr.* **24**: 57–68.
- Howell, E.A., Kobayashi, D.R., Parker, D.M., Balazs, G.H., and Polovina, J.J. (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endanger. Species Res.* **5**: 267–278.
- Janitza, S., Strobl, C., and Boulesteix, A.-L. (2013) An AUC-based permutation variable importance measure for random forests. *BMC Bioinformatics* **14**: 119.
- Johnson, D.S., London, J.M., Lea, M.-A., and Durban, J.W. (2008) Continuous-time correlated random walk model for animal telemetry data. *Ecology* **89**: 1208–1215.
- Jonsen, I.D., Flemming, J.M., and Myers, R.A. (2005) Robust state–space modeling of animal movement data. *Ecology* **86**: 2874–2880.
- Jonsen, I.D., Myers, R.A., and Flemming, J.M. (2003) Meta-analysis of animal movement using state-space models. *Ecology* **84**: 3055–3063.
- Julian, F. and Beeson, M. (1998) Estimates of marine mammal, turtle, and seabird mortality for two California gillnet fisheries: 1990-1995. *Fish. Bull.* **96**: 271–284.
- Komoroske, L.M. and Lewison, R.L. (2015) Addressing fisheries bycatch in a changing world. *Front. Mar. Sci.* **2**: 1–11.
- Kuhn, M. (2013) Package “caret”: Classification and regression training. R package version 6.0-64.
- Larsen, F., Eigaard, O.R., and Tougaard, J. (2007) Reduction of harbour porpoise (*Phocoena phocoena*) bycatch by iron-oxide gillnets. *Fish. Res.* **85**: 270–278.
- Lewison, R., Hobday, A.J., Maxwell, S., Hazen, E., Hartog, J.R., Dunn, D.C., et al. (2015) Dynamic ocean management: Identifying the critical ingredients of dynamic approaches to ocean resource management. *Bioscience* **65**: 486–498.



- Lynn, R.J. and Simpson, J.J. (1987) The California current system: The seasonal variability of its physical characteristics. *J. Geophys. Res.* **92**: 12.947–12.966.
- Mann, K.H. and Lazier, J.R.N. (2006) Dynamics of marine ecosystems: Biological-physical interactions in the oceans. Third edition. Blackwell Publishing.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**: 1069–1079.
- Martin, S.L., Stohs, S.M., and Moore, J.E. (2015) Bayesian inference and assessment for rare-event bycatch in marine fisheries : a drift gillnet fishery case study. *Ecol. Appl.* **25**: 416–429.
- Maxwell, S.M., Hazen, E.L., Lewison, R.L., Dunn, D.C., Bailey, H., Bograd, S.J., et al. (2015) Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. *Mar. Policy* **58**: 42–50.
- Moore, A.M., Arango, H.G., Broquet, G., Powell, B.S., Weaver, A.T., and Zavala-Garay, J. (2011) The Regional Ocean Modeling System (ROMS) 4-dimensional variational data assimilation systems. Part I - System overview and formulation. *Prog. Oceanogr.* **91**: 34–49.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E., and Fryxell, J.M. (2004) Extracting more out of relocation data: Building movement models as mixtures of random walks. *Ecology* **85**: 2436–2445.
- Murray, K. and Orphanides, C. (2013) Estimating the risk of loggerhead turtle *Caretta caretta* bycatch in the US mid-Atlantic using fishery-independent and -dependent data. *Mar. Ecol. Prog. Ser.* **477**: 259–270.
- Murray, K.T. (2009) Characteristics and magnitude of sea turtle bycatch in US mid-Atlantic gillnet gear. *Endanger. Species Res.* **8**: 211–224.
- National Marine Fisheries Service (2013) Biological Opinion on the continued management of the drift gillnet fishery under the Fishery Management Plan for U.S. west coast fisheries for highly migratory species. Available from [http://www.westcoast.fisheries.noaa.gov/publications/protected\\_species/marine\\_mammals/memo\\_signed\\_dgn\\_biop\\_050213.pdf](http://www.westcoast.fisheries.noaa.gov/publications/protected_species/marine_mammals/memo_signed_dgn_biop_050213.pdf)

- Phillips, S.J., Anderson, R.P., and Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**: 231–259.
- Phillips, S.J. and Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography (Cop.)*. **31**: 161–175.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., and Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* **19**: 181–197.
- R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Read, A.J. (2008) The looming crisis: interactions between marine mammals and fisheries. *J. Mammal.* **89**: 541–548.
- Read, A.J., Drinker, P., and Northridge, S. (2006) Bycatch of marine mammals in U.S. and global fisheries. *Conserv. Biol.* **20**: 163–169.
- Rivera K. and Wohl, K.D. (1999) The FAO seabird initiative – international efforts to reduce seabird bycatch in the longline fisheries: what does that mean at home? An Alaskan perspective. *Marine Technology Society Journal* 33:85-87.
- Roe, J.H., Morreale, S.J., Paladino, F. V., Shillinger, G.L., Benson, S.R., Scott, A., et al. (2014) Predicting bycatch hotspots for endangered leatherback turtles on longlines in the Pacific Ocean. *Proc. R. Soc. B* **281**: 20132559.
- Sampson, D.B. (2011) The accuracy of self-reported fisheries data: Oregon trawl logbook fishing locations and retained catches. *Fish. Res.* **112**: 59–76.
- Schwing, F., Murphree, T., and Green, P.. (2002) The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. *Prog. Oceanogr.* **53**: 115–139.
- Schwing, F.B. and Mendelssohn, R. (1997) Increased coastal upwelling in the California Current System. *J. Geophys. Res.* **102**: 3421.
- Seminoff, J.A., Zárate, P., Coyne, M.S., Foley, D., Parker, D., Lyon, B.N.B., and Dutton, P.H. (2008) Post-nesting migrations of Galápagos green turtles *Chelonia mydas* in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data. *Endanger. Species Res.* **4**: 57–72.

- Sepulveda, C.A., Heberer, C., and Aalbers, S.A. (2014) Development and trial of deep-set buoy gear for sword fish, *Xiphias gladius*, in the Southern California Bight. *Mar. Fish. Rev.* **76**: 28–36.
- Shillinger, G.L., Swithenbank, A.M., Bailey, H., Bograd, S.J., Castelton, M.R., Wallace, B.P., et al. (2011) Vertical and horizontal habitat preferences of post-nesting leatherback turtles in the South Pacific Ocean. *Mar. Ecol. Prog. Ser.* **422**: 275–289.
- Sims, M., Cox, T., and Lewison, R. (2008) Modeling spatial patterns in fisheries bycatch: improving bycatch maps to aid fisheries management. *Ecol. Appl.* **18**:649-661.
- Soykan, C.U., Eguchi, T., Kohin, S., and Dewar, H. (2014) Prediction of fishing effort distributions using boosted regression trees. *Ecol. Appl.* **24**: 71–83.
- Starbird, C.H., Baldrige, A., and Harvey, J.T. (1993) Seasonal occurrence of leatherback sea turtles (*Dermochelys coriacea*) in the Monterey Bay region, with notes on other sea turtles, 1986-1991. *Calif. Fish Game* **79**: 54–62.
- Stokland, J.N., Halvorsen, R., and Støa, B. (2011) Species distribution modelling—Effect of design and sample size of pseudo-absence observations. *Ecol. Modell.* **222**: 1800–1809.
- Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., and Zeileis, A. (2008) Conditional variable importance for random forests. *BMC Bioinformatics* **9**: 307.
- Strobl, C., Boulesteix, A.-L., Zeileis, A., and Hothorn, T. (2007) Bias in random forest variable importance measures: illustrations, sources and a solution. *BMC Bioinformatics* **8**: 25.
- Tapilatu, R.F., Dutton, P.H., Tiwari, M., Wibbels, T., Ferdinandus, H. V, Iwanggin, W.G., and Nugroho, B.H. (2013) Long-term decline of the western Pacific leatherback, *Dermochelys coriacea*: a globally important sea turtle population. *Ecosphere* **4**: 1–15.
- VanDerWal, J., Shoo, L.P., Graham, C., and Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecol. Modell.* **220**: 589–594.
- Wallace, B.P., Lewison, R.L., McDonald, S.L., McDonald, R.K., Kot, C.Y., Kelez, S., et al. (2010) Global patterns of marine turtle bycatch. *Conserv. Lett.* **3**: 131–142.
- Wisz, M.S. and Guisan, A. (2009) Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC Ecol.* **9**: 8.

Xie, L. and Hsieh, W.W. (1995) The global distribution of wind-induced upwelling. *Fish. Oceanogr.* **4**: 52–67.

Zydelis, R., Lewison, R.L., Shaffer, S.A., Moore, J.E., Boustany, A.M., Roberts, J.J., et al. (2011) Dynamic habitat models: using telemetry data to project fisheries bycatch. *Proc. R. Soc. B Biol. Sci.* **278**: 3191–3200.

Author Manuscript

Table 1. Environmental variables used for modeling leatherback turtle foraging habitat, their abbreviations, source satellite, and sensor names in parentheses. AVHRR: Advanced Very High Resolution Radiometer, MODIS: Moderate Resolution Imaging Spectroradiometer, AMSR-E: Advanced Microwave Scanning Radiometer, SeaWiFS: Sea-viewing Wide Field-of-view Sensor, ASCAT: Advanced Scatterometer, POES: Polar-orbiting Operational Environmental Spacecraft, QuikSCAT: Quick Scatterometer, METOP: Meteorological operational satellite

Variable name (abbreviation)	Satellite (sensors)
Sea Surface Temperature (SST)	
SST1	NOAA-17 and NOAA-18 polar orbiting spacecraft (AVHRR)
SST2	Aqua (MODIS, Aqua), NOAA GOES-10, GOES-12 (GOES), NOAA POES-17, and POES-18 (AVHRR)
Geostrophic current (UGEO and VGEO)	TOPEX/Poseidon, ERS-1, ERS-2, Geosat Follow-On, Envisat, Jason-1 (Altimeter)
Wind (wekm)	
Wind1	QuikSCAT (SeaWinds)
Wind2	METOP (ASCAT)
Primary Productivity (PP)	GeoEye Orbview-2 (SeaWiFS), NOAA-POES (AVHRR) NASA Aqua (MODIS)
Sea Surface Height (SSH)	JASON-1, TOPEX/POSEIDON, ENVISAT, GFO, ERS ½, GEOSAT (Altimetry sensors on multiple spacecraft)

Table 2. Model definitions and  $\Delta$ DIC values for modeling the entry of leatherback turtles into the PLCA using the BLMM approaches. UW36s\_60d and UW36s\_90d = standard deviation of upwelling at 36°N over 60 and 90 days, respectively; UW39cumu = cumulative upwelling at 39°N; BLMM = Bayesian linear mixed-effects model.

		BLMM
Model	Definition	$\Delta$ DIC
4	UW36s_60d + UW39cumu	0.00
3	UW39cumu	204.24
1	UW36s_90d	298.41
2	UW36s_60d	324.85

Table 3. Estimated coefficients, SEs, and approximate 95% posterior intervals for the best logistic regression model (Model 4) for the analysis of predicting the entry of leatherback turtles to the PLCA. UW36s\_60d = standard deviation of upwelling at 36°N over 60 days, UW39cumu = cumulative upwelling at 39°N, s = the standard deviation of the individual random effects.

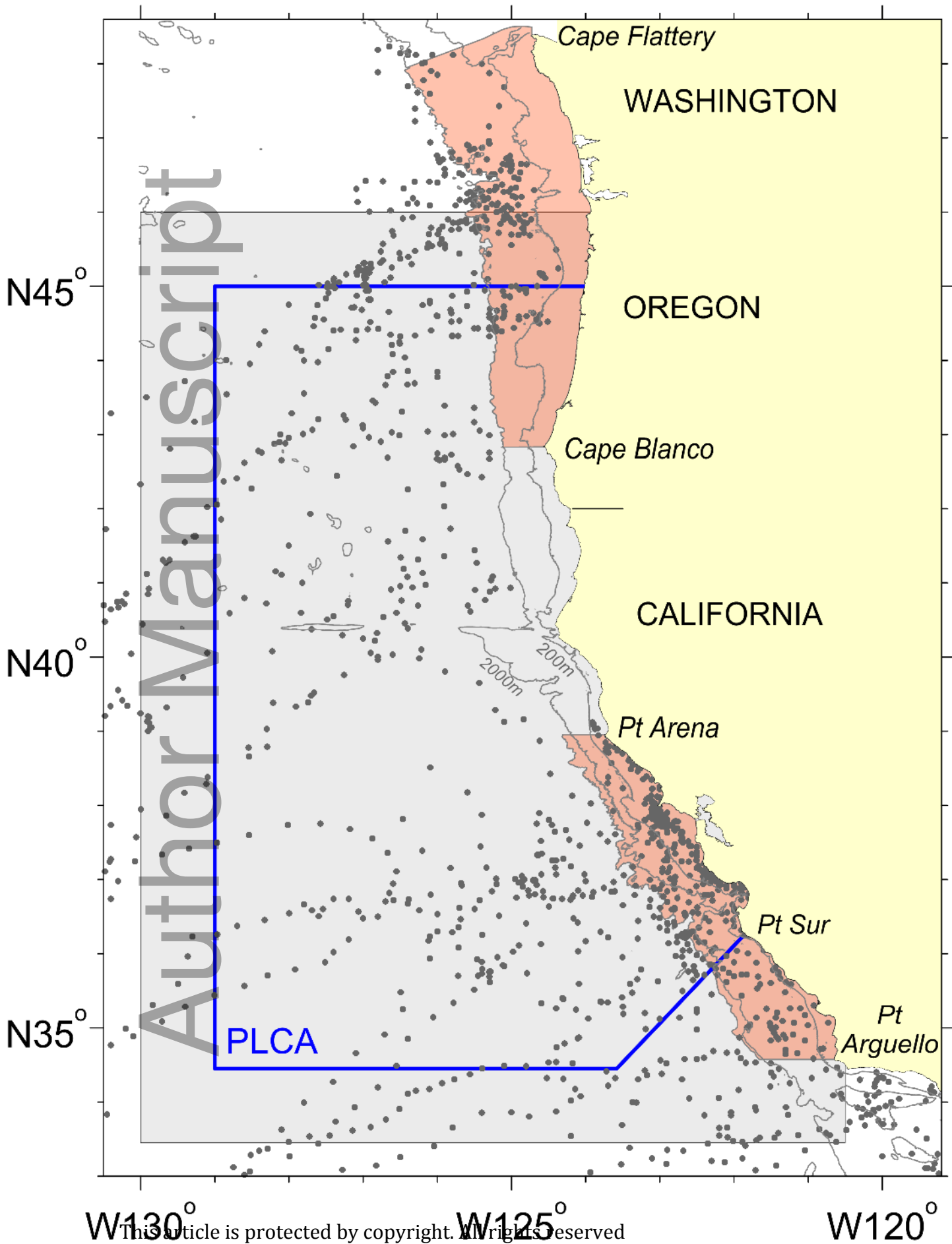
Model 4			
	Median	2.5%	97.5%
Intercept	6.68	-7.39	19.72
UW36s_60d	-6.06	-11.02	-2.00
UW39cumu	30.50	22.02	40.55
s	31.16	19.17	53.85

Table 4. Model definitions and  $\Delta$ DIC values for modeling the departure of leatherback turtles from the PLCA using the BLMM approach. UW48mean\_60d = mean upwelling at 48°N over 60 days, PDO = Pacific Decadal Oscillation Index. The product model (Model 4) includes linear terms also, i.e., UW48mean\_60d + PDO + UW48mean\_60d:PDO.

Model	Definition	$\Delta$ DIC
3	UW48mean_60d + PDO	0.00
4	UW48mean_60d * PDO	34.12
1	UW48mean_60d	131.56

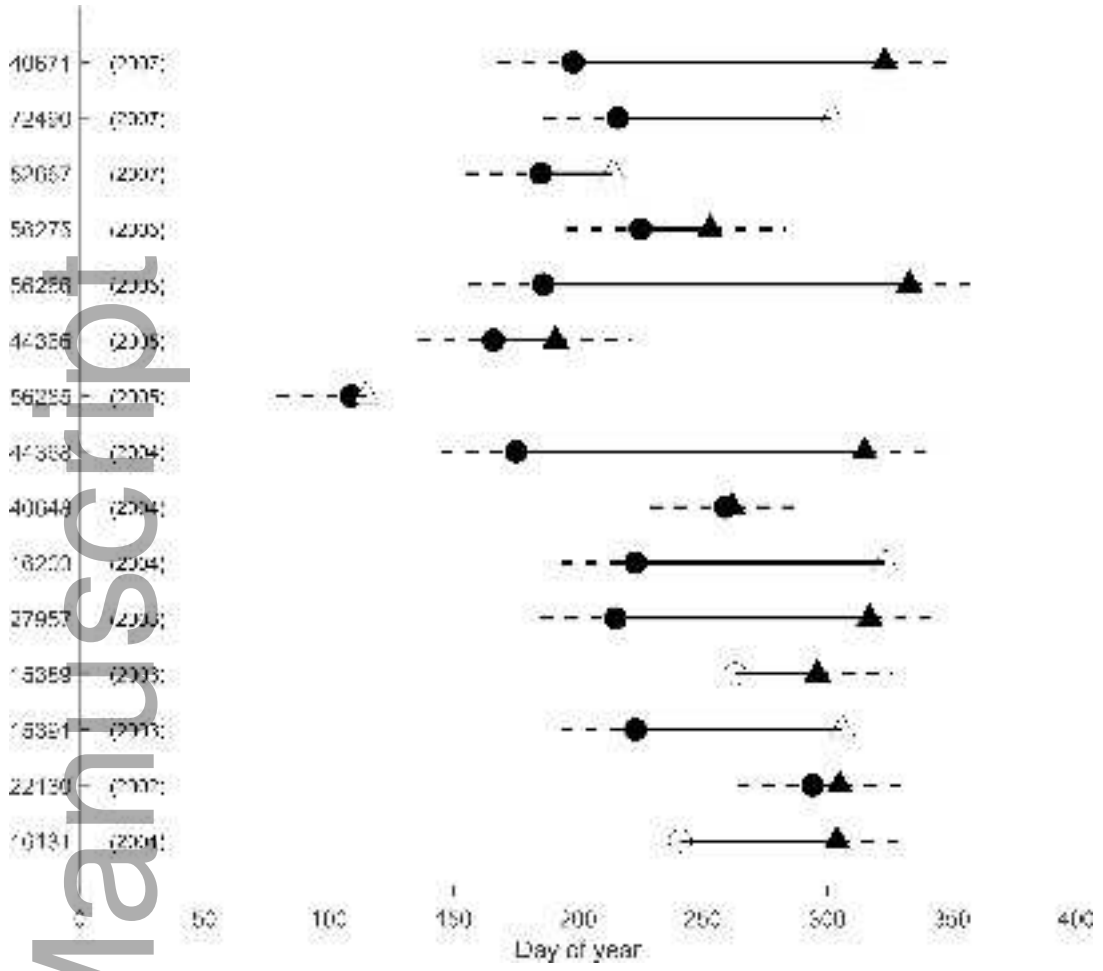
Table 5. Estimated coefficients, SEs, and approximate 95%PI for the best logistic regression model (Model 3) for the analysis of predicting the departure of leatherback turtles from the PLCA. UW48mean\_60d = mean upwelling at 48°N over 60 days, s = standard deviation of the individual random effects.

	Median	2.5%	97.5%
Intercept	1.37	-5.37	8.13
PDO	-7.86	-11.04	-5.15
UW48mean_60d	15.54	11.89	19.89
s	9.12	5.22	8.13

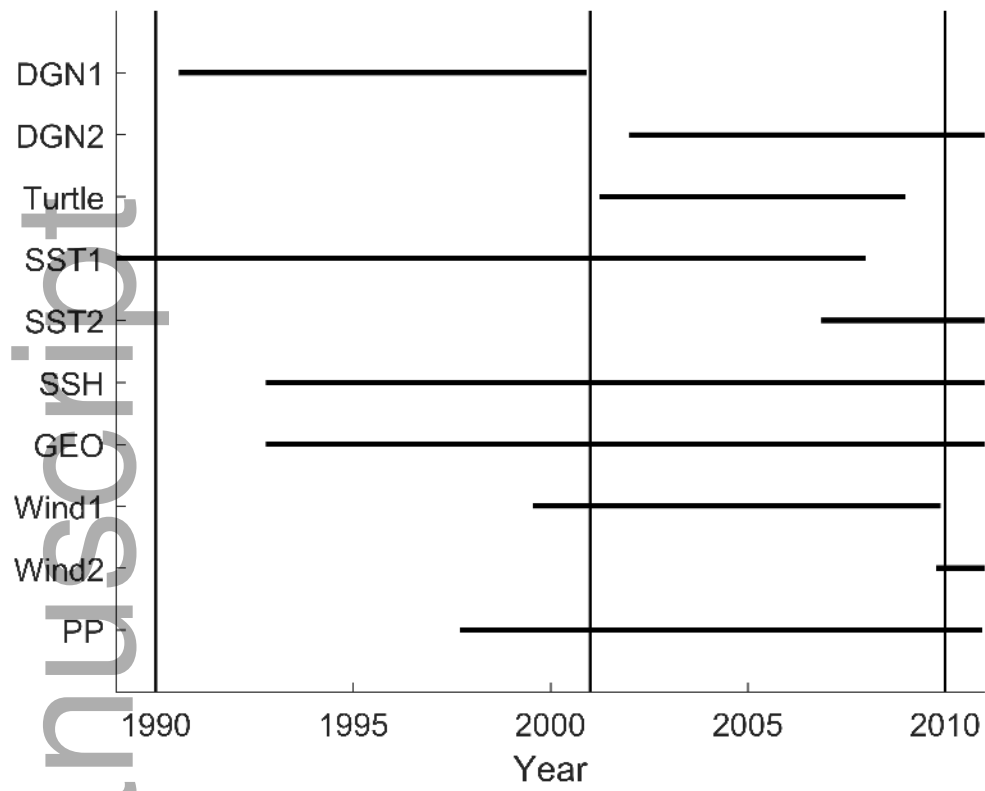


This article is protected by copyright. All rights reserved

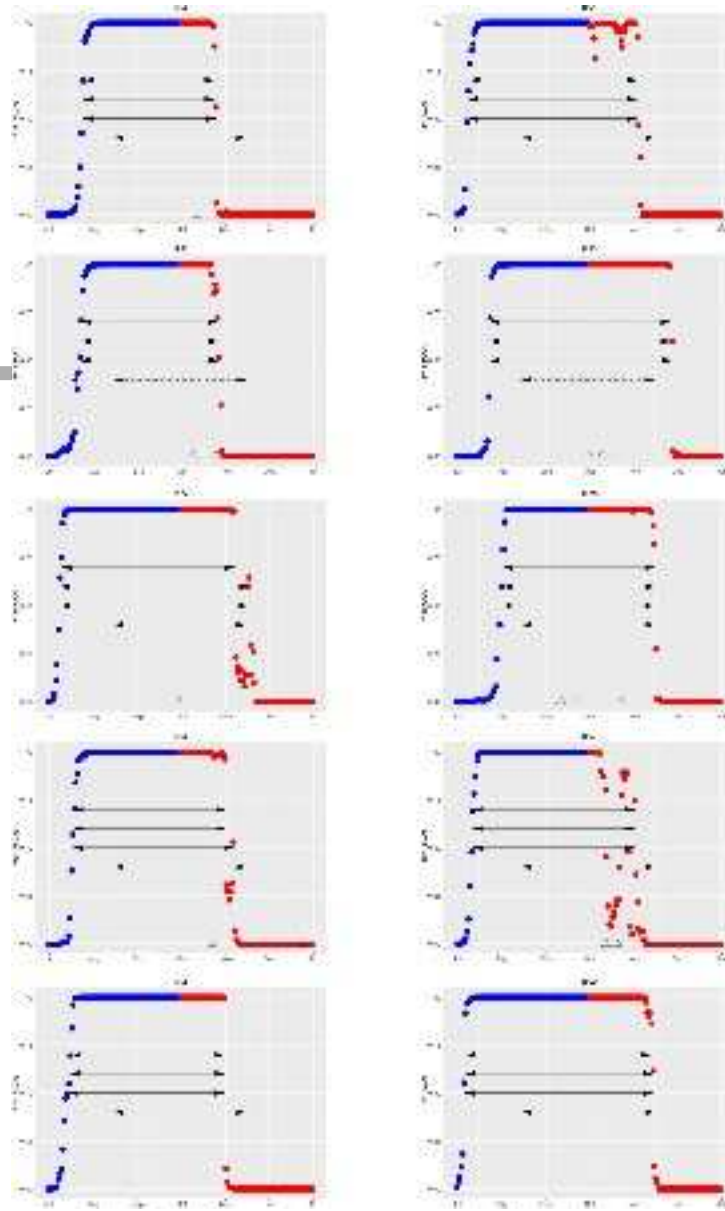




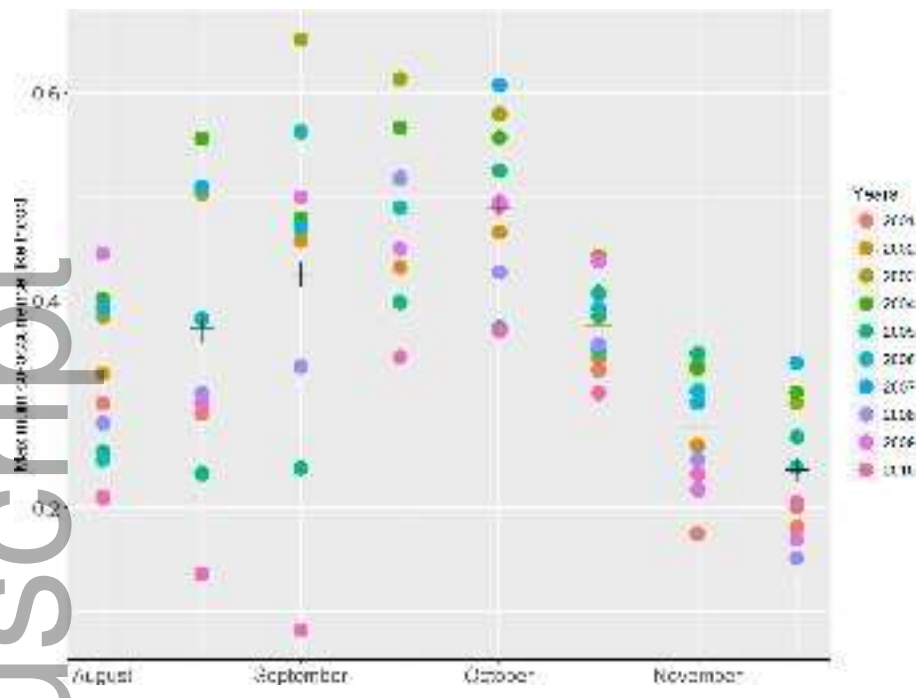
fog\_12181\_f2.tif



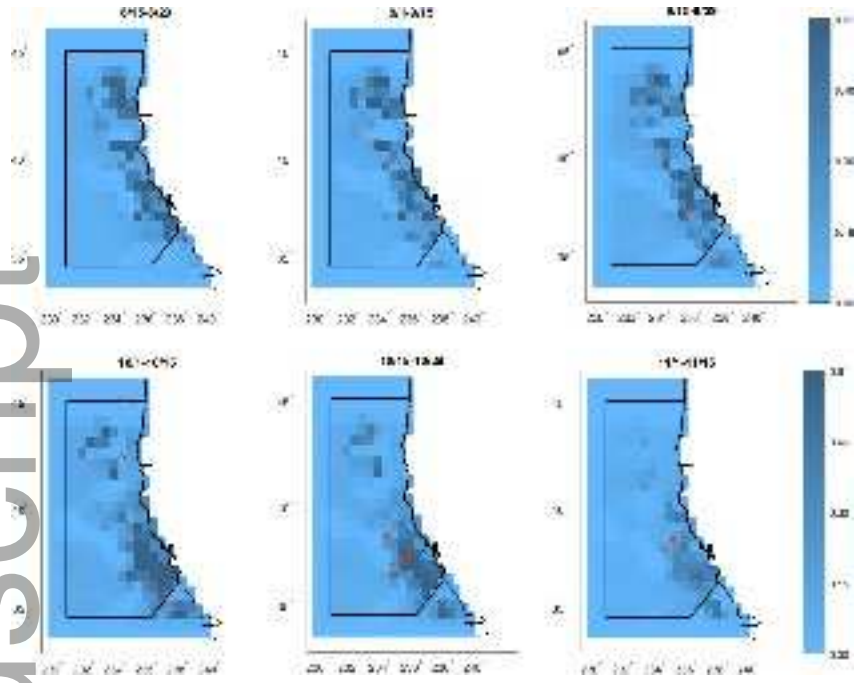
fog\_12181\_f3.tif



fog\_12181\_f4.tiff



fog\_12181\_f5.tiff



fog\_12181\_f6.tif