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Climate change impacts on leatherback turtle pelagic habitat in the southeast Pacific

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Abstract

Eastern Pacific populations of the leatherback turtle (*Dermochelys coriacea*) have declined by over 90% during the past three decades. The decline is primarily attributed to human pressures, including unsustainable egg harvest, development on nesting beaches, and by-catch mortality. In particular, the effects of climate change may impose additional stress upon already threatened leatherback populations. This study analyzes how the pelagic habitat of Eastern Pacific leatherbacks may be affected by climate change over the next century. This population adheres to a persistent migration pattern; following nesting at Playa Grande, Costa Rica, individuals move rapidly through equatorial currents and into foraging habitat within the oligotrophic South Pacific Gyre. Forty-six nesting females were fitted with satellite tags. Based on the turtle positions, ten environmental variables were sampled along the tracks. Presence/absence habitat models were created to determine the oceanographic characteristics of the preferred turtle habitat. Core pelagic habitat was characterized by relatively low sea surface temperatures and chlorophyll-a. Based on these habitat models, we predicted habitat change using output from the Geophysical Fluid Dynamics Laboratory prototype Earth System Model under the Special Report on Emissions Scenario's A2 (business-as-usual) scenario. Although the model predicted

both habitat losses and gains throughout the region, we estimated that overall the core pelagic habitat of the Eastern Pacific leatherback population will decline by approximately 15 percent within the next century. This habitat modification might increase pressure on a critically endangered population, possibly forcing distributional shifts, behavioral changes, or even extinction.

Keywords: climate changes, migratory species, aquatic reptiles, pelagic environment, habitat selection

Abbreviations: Satellite Relay Data Logger (SRDL), Smart Position Only Tag (SPOT), Geophysical Fluid Dynamics Laboratory (GFDL), Correlated Random Walk (CRW), Generalized Additive Mixed Model (GAMM), Generalized Additive Model (GAM), Sea Surface Height root mean square (SSHRMS), bathymetry (bathy), bathymetry root mean square (bathyrms)

1. Introduction

Climate change's impact on migratory species is difficult to predict. Unlike resident species, they travel long distances, increasing their exposure to regions that will likely be affected by climate change (Robinson et al., 2008). On the other hand, migratory species have acclimated to various habitats to complete their seasonal or inter-annual journeys; thus, they may be able to adapt to climate fluctuations (Robinson et al., 2008). Climate change adaptations, such as range shifts and altered phenology, have already been documented in migratory species (Walther et al., 2002). However, migratory species with low genetic variability and long generation times are unable to rapidly adapt to a changing climate (Robinson et al., 2008). Particularly for threatened and endangered species, this potential inability to adapt to habitat losses could further increase population declines (Burrows et al. 2011; Hazen et al., 2013).

The Intergovernmental Panel on Climate Change (IPCC) generated six climate change scenario families based on several hypothetical futures characterized by varying levels of greenhouse gas emissions (IPCC, 2000). The six potential scenario families projected an average sea surface temperature rise of 1-6°C by 2100 using an ensemble of 23 models (IPCC, 2007). As temperatures rise, ocean conditions will alter including changes in ocean currents, nutrient availability, water column stratification, the spatial distribution of primary production, and relative abundance and species composition (Hoegh-Guldberg and Bruno, 2002; Fogg, 1991; Hinder et al., 2012). Temperature changes will most likely affect marine ectotherms more directly than other species because they already occupy the entirety of their thermal tolerance range, i.e. the extent of their latitudinal habitat based on their temperature tolerance (Sunday et al., 2012).

Leatherback sea turtles (*Dermochelys coriacea*) are the largest living turtle and among the largest living reptiles (Paladino et al., 1990). They are a late-maturing, long-lived species (Hawkes et al. 2009; Avise et al. 1992). Leatherbacks utilize their large body size, blood flow regulation, and changes in swimming speed and activity to regulate internal temperatures (Paladino et al., 1990; Bostrom and Jones, 2007; Bostrom et al., 2010). Leatherbacks are distributed globally and every population undergoes long-distance migrations, traveling from

breeding habitats to foraging grounds (Benson et al., 2007; Shillinger et al., 2008; Shillinger et al., 2011; Fossette et al., 2010; Benson et al., 2011).

The Eastern Pacific leatherback population is distinctive because the population has a persistent migration pattern; female turtles follow a specific migratory corridor and seem to use similar foraging areas (Shillinger et al., 2008). The main nesting population in the Eastern Pacific is located in Playa Grande, Costa Rica (Spotila et al., 1996). At the end of the nesting season, females move rapidly south through strong equatorial currents and disperse into the vast South Pacific Gyre, characterized by low ocean energy and low productivity (Shillinger et al., 2008). In their foraging grounds, the population may feed on gelatinous zooplankton (i.e. jellyfish); although much of their ecology still remains a mystery (Fossette et al., 2011; Heaslip et al., 2012).

Leatherbacks are of conservation concern due to development on nesting beaches, illegal egg harvesting, and fisheries by-catch, which is considered the main driver behind leatherback population declines (Hammann et al., 2000). Approximately 1,500 Pacific female leatherbacks were killed every year in longline and driftnet fisheries during the 1990s (the total population was 34,500 in 1996; Spotila et al., 1996), which drove Eastern Pacific leatherbacks to the verge of extinction (Spotila et al., 2000). In the past three decades, the Eastern Pacific population has declined by over 90 percent (Spotila et al., 2000; Santidrián Tomillo, et al., 2007) and climate change may exacerbate these population declines (Saba et al., 2012). For instance, population dynamic models project that temperature increases may reduce Costa Rican leatherbacks hatching success and hatchling emergence rate by more than 50 percent over the next 100 years due to warming of the nesting beach and changes in rainfall (Saba et al., 2012). However, recent studies only consider climate change impacts on the Eastern Pacific population's nesting grounds. To fully understand how climate change will impact Eastern Pacific leatherbacks, habitat changes need to also be quantified in their migratory and foraging habitat.

This study evaluates projected impacts of climate change on Eastern Pacific leatherbacks' primary pelagic habitat to forecast vulnerable leatherback habitat and to potentially inform adaptive management strategies and conservation efforts. We also assess the hypothesis that

climate change may transform previously undesirable environments into beneficial leatherback habitats (Robinson et al., 2008).

2. Methods

2.1 Tagging and data processing

Female leatherback sea turtles were instrumented with either a Sea Mammal Research Unit (SMRU) Satellite Relay Data Logger (SRDL) tag (n=36) or a Wildlife Computer Smart Position Only (SPOT) tag (n=10) from 2004 to 2007 (Shillinger et al., 2008). The SRDL tags were programmed to transmit position, temperature, dive data, and tag diagnostic information. The SPOT tags were programmed to collect position data. The satellite transmitters were mounted on the turtles during oviposition using a harness technique (Eckert, 2002). Data from the tags were transmitted via radio signals sent to the Argos satellite system (Argos, 2007). Final position estimates were generated at daily intervals using a switching state-space model (SSSM), which was applied to the raw Argos position data. The SSSM incorporated the measurement error in Argos telemetry data to improve position estimates (Jonsen et al., 2007; Shillinger et al., 2011; Bailey et al., 2012).

For each of the 46 leatherback tracks, 150 correlated random walks (CRWs) were created. CRWs are paths that consist of a succession of random steps. The leatherbacks' position was interpolated every six hours based on the mean number of raw locations per day using a state-space model. Each CRW step is randomly sampled from the distributions of distance and turning angle simultaneously, which are derived from the original leatherback track. Consistent with the 46 tracks, the CRWs starting point was at Playa Grande, Costa Rica. Each CRW's initial direction matched its corresponding tag while the speed and turning angle were chosen together randomly from the tag's entire movement distribution (Figure 1S). The CRWs serve as pseudo-absences and describe a null model where turtles could travel independent of oceanographic parameters and ecological forcing. Comparing environmental parameters along the CRWs to those along the actual leatherback tracks can test whether leatherbacks are selecting for specific oceanographic features. Pseudo-absences are however not true absences because the migration

pathway of untagged leatherbacks is unknown and untagged turtles may have potentially followed a CRW track. However, Wisz and Guisan (2009) determined that randomly selected pseudo-absences can successfully identify the importance of predictor variables for highly mobile species if true absence data is unavailable. The suite of CRWs were flagged and ranked based on the similarity to the actual track in angle and distance traveled (from the starting point to the end point); the lower the flag value, the more similar the CRW was to the leatherback track's total distance and angle. Twenty-five percent of the highest CRW flag values per leatherback track were removed from the analysis to exclude the most dissimilar tracks, accounting for leatherback turtles known migration patterns (Figure 2S).

2.2 Satellite-derived environmental data

Remotely sensed environmental data were obtained for both the leatherback and CRW tracks using Xtractomatic (http://coastwatch.pfel.noaa.gov/xtracto/). The data sets included time-series of sea surface temperature (SST), surface chlorophyll -a (chl a) concentration, sea surface height (SSH), SSH variability (root mean square, SSHRMS), vertical current due to Ekman pumping (wekm), SST frontal probability index (FPI), bathymetry (bathy), and rugosity (bathyRMS). These variables have been previously explored as important for leatherbacks in the Southeast Pacific as they are important proxies for ocean features (SSH, SSHRMS, wekm, FPI, bathy, bathyRMS), physiological constraints (SST), and forage base (chl a; Shillinger et al., 2011, Bailey et al. 2012). Estimates of zooplankton distribution globally show similar patterns to chlorophyll (Strömberg et al. 2009), but there are no data currently available on the prey field. For each oceanographic parameter, a mean value was calculated within a box based on the mean latitude and longitude error (0.2° longitude \times 0.2° latitude \times (5 to 10 day intervals)) and centered at the position of each daily SSSM-interpolated turtle position (Shillinger et al., 2011). Transformations of the parameters were explored to ensure data were normally distributed. A logarithmic transformation was required for chl a and FPI and a square root transformation for SSHRMS and bathyRMS.

2.3 Habitat Model Generation

In order to compare oceanographic parameters along the leatherback and CRW tracks, a binary presence/absence model with a negative binomial link function was used. Primary leatherback habitat may be determined if certain oceanographic features correlate with leatherback turtle presence (Redfern et al., 2006). Generalized additive mixed models (GAMMs) were constructed to analyze the statistical correlation between the eight oceanographic parameters described above and leatherback presence/absence (Wood, 2006). GAMMs are semi-parametric models that automatically identify the distribution of the dependent parameter and apply an additive function to determine the variables' response to predictors (Bolker et al, 2009; Guisan et al., 2002). GAMMs allow for non-linearity, non-constant variance, and non-monotonicity (Guisan et al., 2002). The model is useful because it incorporates random effects and applies a grouping variable to account for correlations between observations (e.g. correlation between points on an individual leatherback track; Bolker et al., 2009).

The GAMMs linked the environmental covariates to leatherback presence/absence (leatherback track/randomly chosen CRW). Various combinations of the eight environmental data sets were included in the GAMMs to determine the most robust model. The models' robustness was compared using backwards and forward selection techniques with Akaike Information Criterion (AIC) and adjusted r-squared values (Akaike, 1974). The GAMMs were run in R (version 2.11) using the MGCV package (version 1.7-6). The GAMM model with the highest AIC and r-squared value was run 100 times with randomly chosen CRW tracks for each tag to examine the persistence in its significance.

Predictive Generalized Additive Models (GAMs), which included SST and log chl a, were generated for each decade from 2001 to 2100. SST and log chl a are the two variables that have been predicted until 2100 and were accordingly included in the predictive GAMs. The traditional GAMM established preferred leatherback habitat by determining SST and chl a values associated with leatherback turtle presence. The predictive GAMs used the fitted GAMM model to compare preferred leatherback habitat to forecasted SST and chl a values (Wood, 2011). The predictive GAM results revealed changes in leatherbacks' pelagic habitat over time. The change in the likelihood of an area being leatherback habitat over the next century was determined by subtracting the average habitat likelihood (scale of 0-1) from 2080-2100 from the 2001-2020

averages. The spatial limits of the predictive habitat model were from 20° N to 40° S and 140° W to 70° W; Eastern Pacific leatherbacks' migration and foraging habitats were respectively defined as being north or south of approximately 8° S (identified by a previous SSSM; Shillinger et al., 2011).

Core leatherback habitat was defined as the top 25% of all habitat (see Hazen et al. 2013). The number of cells (1° spatial grid size) considered core habitat were averaged on a monthly, yearly, and 5-year mean time series from 2001-2100. Confidence intervals were calculated using a bootstrap approach, fitting and predicting GAMs with randomly selected CRWs for each leatherback track (100 CRWs per track and 4600 model combinations). The standard deviation of the 4600 estimates of predicted habitat change was used to calculate the confidence intervals, indicating how CRW choice influences the GAM results. The mean percent change in core habitat from 2001-2100 was calculated as the change in the ensemble monthly time series values since the first year of the predictive model (2001).

Projected SST and chl a values for the next century under the IPCC's A2 scenario were provided by the Geophysical Fluid Dynamics Laboratory (GFDL) of the National Ocean and Atmospheric Administration's (NOAA) prototype Earth System Model (ESM2.1), that contributed to the Fifth Coupled Model Intercomparison Project (Dunne et al., 2013). ESM2.1 is an atmospheric-ocean general circulation model coupled to a marine biogeochemistry model, allowing predictions of SST and chl a spatial patterns (1° spatial grid size) over time (Delworth et al., 2006). It is important to note that after ESM2.1 was initialized to observations, it was run in free climate mode with only radiative forcing for over a thousand years to reach equilibrium. After the model reached equilibrium, radiative perturbation was undertaken for both historical and future projections. Thus, the model cannot be expected to have the same phasing of internal climate variability as during the historical period or the coming decades. Patterns and trends in satellite and GFDL output from 2001 to 2010 showed no significant biases over space or time (Figure 3S).

3. Results

3.1 GAMM Selection

The Eastern Pacific population's migration pattern consists of directed movements from nesting grounds in Central America, past the equatorial currents, through their migratory habitat (from Playa Grande to 8°S), and into foraging grounds in the South Pacific Gyre (10°S to 35°S, 125°W to 80°W; Shillinger et al., 2008, 2011). The GAMMs determined the oceanographic parameters correlated with tagged Eastern Pacific leatherback habitat as they migrate to their foraging grounds.

The full model included all eight oceanographic parameters as a preliminary exploration of satellite data and was robust (R-squared value = 0.59, Table 1). The five variables that were primarily attributed to leatherback presence were respectively: SST, chl a, SSHRMS, bathyrms, and wekm (Table 1S). Bathymetry was the only parameter included in the initial model that was not significantly associated with leatherback habitat (Figure 4S). However, the only two significant oceanographic parameters utilized from the GFDL ESM2.1 were SST and chl a. With only SST and chl a in the predictive GAMM, the habitat model remained statistically significant (mean R-squared =0.3; Table 1), suggesting that both SST and chl a serve as important proxies for leatherback habitat. The model revealed that the tagged leatherbacks preferred cooler SSTs (< 25 °C) and lower chl a levels (< 0.1 mg/m³) than were available as potential habitat (Figure 1).

3.2 SST and chl a values from 2001-2100

Eastern Pacific SST and chl a values from the 2001-2010 model output were plotted to visualize current leatherback habitat conditions (Figure 2a&b). In comparison to the rest of leatherbacks' habitat, the equator and the South Pacific Gyre were characterized by cooler temperatures (Figure 2a). Chl a levels in the region were lowest in the South Pacific Gyre and highest at the equator (Figure 2b).

The change in SST and chl a over time was plotted by subtracting 2080-2100 SST and chl a values from 2001-2020 levels, minimizing the influence of interannual to decadal variability for the long-term estimate of change (Figure 2c&d). Over the next century, SST is predicted to increase across the majority of Eastern Pacific and remain stable in the eastern portion of

leatherbacks' foraging habitat (south of 8° S; Figure 2a&c). The greatest increases will most likely occur in the tagged leatherbacks' migration habitat (north of 8° S) and between 30°S and 40°S, in the tagged leatherbacks' foraging area (Figure 2c). The GFDL model indicates that chl a values are expected to become more uniform across the entire region. For instance, the greatest chl a increase is predicted to occur in the eastern section of the leatherback population's primary foraging habitat (20°S to 30°S, 125°W to 95°W), where chl a levels are currently the lowest in the region (Figure 2d). Correspondingly, the greatest chl a decrease is expected at the equator, where chl a values are currently the highest in the populations' habitat.

3.3 Predicted Leatherback Habitat from 2001-2100

The predictive GAMs established the likelihood of an area being leatherback habitat from 2001-2100, based on varying SST and chl a values (Figure 3a&b). The region predicted by the model as having the highest likelihood of being habitat from 2001-2010 was within the previously identified leatherback foraging area in the Gyre (20°S to 30°S, 125°W to 95°W, i.e. current primary foraging habitat; Figure 3a; Shillinger et al., 2011).

The predictive model forecasted between a six to ten percent decrease in leatherbacks' early migration habitat (before approximately 2° N, Figure 3b). Up to a four percent decline by cell is expected in leatherbacks' current primary foraging habitat (Figure 3a&b). Habitat gains of up to three percent per cell are expected at the equator, in the regions surrounding current primary foraging habitat, and south of 30 °S (Figure 3b). However, given the uncertainty inherent in the predictive model, these gains may be insignificant.

Model projections indicate that there will be a net loss in Eastern Pacific leatherbacks' core habitat (i.e. where there was over a 75 percent chance of leatherback presence; see Hazen et al. 2013). Over the next century, Eastern Pacific leatherbacks' core pelagic habitat in the south Pacific is predicted to decrease by around 15 percent (Figure 4). The percent change in core habitat is highly variable on a monthly time scale because of seasonal differences in SST and chl a. However, the yearly and five-year percent change in core habitat show a clear, steady decline in leatherback habitat from 2001 to 2100 that may continue beyond the modeling domain.

4. Discussion

4.1 Habitat Model Fit

Eastern Pacific leatherbacks' pelagic habitat was characterized by our model by low SST and chl a levels. Shillinger et al. (2011) also found that the physical variables with the highest correlation to leatherbacks' foraging zone were low SST and chl a, followed by low FPI and SSHRMS (indicating low mesoscale activity). However, Shillinger et al. (2011) analyzed the migration habitat and foraging zone independently. When analyzed independently, the population's migration habitat was characterized by high SST, chl a, and higher mesoscale activity. This study's habitat model concurrently analyzed migration and foraging habitat. The population spent the majority of their tag time in the South Pacific Gyre; consequently, leatherback habitat was primarily associated with physical variables from the leatherbacks' foraging zone.

The habitat model's consistency with Shillinger et al.'s (2011) foraging zone results indicates that the model is likely predicting suitable leatherback habitat based on SST and chl a levels. It is important to note that the area predicted as having the highest likelihood of being suitable habitat is west of the majority of the 46 tagged leatherback tracks (Figure 3A; 20°S to 30°S, 125°W to 95°W). This difference may be a result of only a portion of the Costa Rican nesting population being tagged or that ocean currents make the highest probability habitat inaccessible (Gaspar et al., 2006).

4.2 Influence of SST, chl a, ocean currents, and prey abundance

The overall shift in leatherback habitat was expected as SST is essential in determining the distribution of adult leatherbacks (Spotila and Standora, 1985). However, the effect of climate change on leatherback habitat may vary across populations. Nesting populations from the Western Pacific and Atlantic Oceans might have foraging habitats characterized by different SST and chl a values (Benson et al., 2011). For instance, preferred chl a levels differ between populations' foraging habitats in both the Pacific and North Atlantic; open ocean foraging zones

are characterized by low chl a; while high chl a levels are typical of foraging habitat in coastal regions (e.g., the California Current Ecosystem, Benson et al., 2011; Bailey et al., 2012).

The Western Pacific leatherback population foraging in the California Current Ecosystem utilizes habitat that is characterized by high chl a values (Benson et al., 2011), and a ten percent increase in potential habitat was predicted for this population (Hazen et al., 2013). The contrast between the predicted habitat change in the North Pacific CCE and the Eastern Pacific over the next century may in part be due to the divergent association with chl a values. Furthermore, the GFDL model predicted that chlorophyll in the South Pacific subtropical gyre will increase over the next century, contrary to predictions in the North Pacific (Polovina et al., 2011).

The North Atlantic population is also characterized by relatively higher chl a values and possesses higher foraging success than the Eastern Pacific population (Bailey et al., 2012). Therefore, the North Atlantic population habitat may also not be as affected by climate change as the Eastern Pacific population. These differences reveal that the effects of climate change are more accurately predicted if populations are examined individually; the variations in leatherbacks' preferred environmental conditions would likely be lost if the effects of climate change were analyzed at the species level.

Although SSTs and chl a levels are important in determining leatherback distribution, leatherback migration patterns are also affected by currents (Gaspar et al., 2006). It is expected that ocean current behavior patterns will alter with climate change (Hoegh-Guldberg and Bruno, 2002), however our predictive model could not take into account potential current speed and directional changes. These might be important parameters to consider in future models; as equatorial currents change and strengthen, leatherback migration patterns may be impacted even further and potentially constrain turtles to increase their swimming speed, expending additional energy, to reach their foraging grounds (e.g. Galli et al., 2012 for similar considerations in the North Atlantic).

Changing SSTs, chl a levels, and currents may also affect the distribution and abundance of leatherback prey and therefore leatherback foraging behavior. Despite the lack of distributional

data on gelatinous zooplankton, it is well known that these organisms are also influenced by oceanographic parameters and may respond to climate shifts (Richardson et al., 2009; Brotz et al., 2012). Foraging success is suspected to be low in the Southeast Pacific (Bailey et al., 2012), but it might change if oceanographic conditions are modified. The relationship between zooplankton distribution and oceanographic conditions is not clearly understood; therefore, climate change may positively or negatively affect the population's foraging success.

Leatherbacks' foraging success is directly tied to their nesting success as females require a specific amount of energy for beginning reproduction (Saba et al., 2007). Changes in foraging habitat and potentially foraging success may thus have population level effects via variations in annual egg production.

4.3 Habitat Changes

The approximate 15 percent loss in Eastern Pacific leatherback habitat may force the population to shift west or south of their current foraging habitat to regions where there is a predicted habitat gain over the next century. In the North Atlantic, the 15°C isotherm has moved north by 330 km since 1983; consequently the Atlantic leatherback populations have expanded their range further north (McMahon and Hays, 2006). Under the A2 emissions scenario, the Pacific Ocean's 15°C isotherm is also predicted to move toward the poles (Poloczanska et al., 2009). Eastern Pacific leatherbacks' cold thermal tolerance boundary is currently around 37°S (i.e. 14°C; Shillinger et al., 2011) but with increasing SSTs, the population could expand further south.

Poleward migrations, in response to climate change, are expected to reduce survival rates for less mobile species (Hansen et al., 2006). Leatherbacks are, however, long-distance migrants and they have a broad thermal range that might allow them to benefit from a slight range expansion (Cheung et al., 2009). Additionally, the Eastern Pacific population's habitat is only known for the first year of its four-year migration period; the population may be already exploiting regions that this study did not define as current leatherback habitat.

Leatherbacks may be able to expand their range into new regions; however, the predicted habitat gains may not be significant enough to compensate for the habitat loss. Although marine top

predators tend to exhibit plasticity to changing environments, the Eastern Pacific leatherbacks' possess low genetic variability (Dutton et al., 1999). Low genetic variation and long generation times are associated with low resistance to stressful conditions (Hoffmann and Sgró, 2011). Therefore, behavioral and physiological adaptation may be difficult for the Eastern Pacific leatherbacks as climate change progresses. Ultimately, ecosystem-based models that can estimate habitat based on movement capabilities, physiological needs, and forage landscape will be necessary to develop a more mechanistic approach as these data become available (e.g. Lehodey et al., 2010).

4.4 Conservation Strategies

Over the coming century, the Costa Rican nesting population is already expected to experience a seven percent decline per decade because of a 50 to 60 percent reduction in egg and hatchling survival as climate change progresses (Saba et al., 2012; Santidrián Tomillo et al., 2012). This study indicates that Eastern Pacific leatherbacks' pelagic habitat will also be affected by climate change. With the population already facing a suite of pressures including bycatch, beach development, and poaching, the potential reduction in suitable pelagic habitat will add stress to an already vulnerable population.

To counteract the impacts of climate change and reduce the population's decline, flexible and dynamic adaptive management strategies are needed. Conservation programs at nesting beaches have been employed since the 1950s and need to be strengthened, but marine conservation strategies, involving both neritic inter-nesting and foraging habitats (Shillinger et al., 2010) and more remote pelagic migration and foraging habitats, are not as well established (Frazier, 2002). The difficulty with conservation in pelagic habitats is the lack of national boundaries. Intergovernmental cooperation is needed to mandate such international policies (Hamann et al., 2010).

This study identified Eastern Pacific leatherback habitat that may be affected by climate change and in particular regions with the greatest potential habitat gains. This spatial analysis provides a

first step to allow conservation managers to identify regions where the establishment of pelagic protected areas might be the most effective as marine ecosystems shift.

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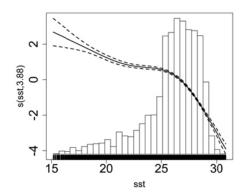
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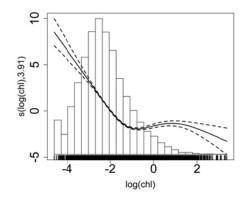
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Table 1: P-value, R squared, and AIC for the GAMM that included all eight parameters (full model) and the SST and chl a GAMM (predictive model).





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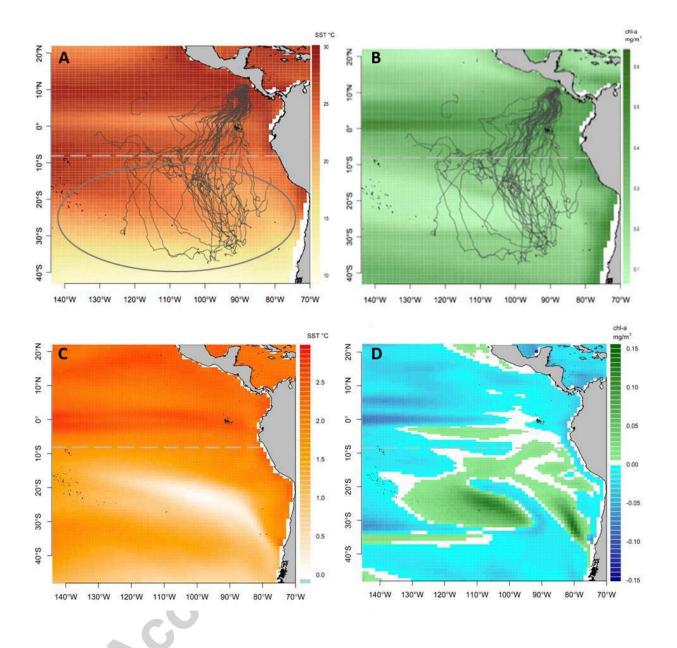


Figure 2: a) average SST (°C) from 2001-2010 (grey circle indicates the South Pacific Gyre), b) average chlorophyll a level from 2001-2010, c) change in SST over the next century (average SST from 2080-2100 subtracted from the average SST from 2001-2020), d) change in chl a over the next century (average chl a from 2080-2100 subtracted from the average chl a from 2001-2020) all from GFDL climate model output. Dark grey lines represent the 46 tagged leatherback tracks. Dashed grey line separates the migration habitat (north of 8°S) and foraging habitat (south of 8°S).

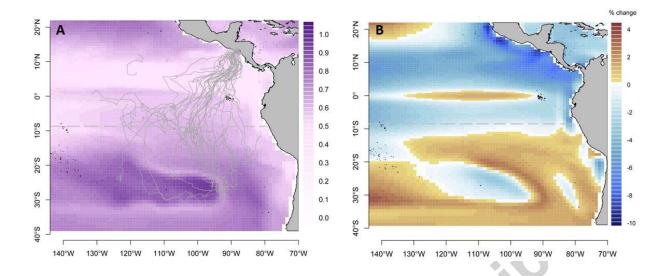
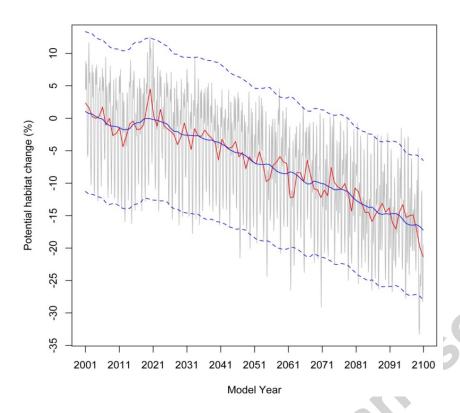


Figure 3: a) Current leatherback habitat, the darker the purple the higher the probability of leatherbacks occupying the area (scale of 0 to 1). Dark grey lines represent the 46 tracks. b) Change in the likelihood of an area being leatherback habitat (in percent). A decrease in habitat is represented by a darker blue while an increase is shown in red. Dashed grey line separates the migration habitat (north of 8°S) and foraging habitat (south of 8°S).



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Figure 4: Overall change in predicted core habitat from 2001-2100. The grey line is the average monthly percent change in core habitat, the red line is the average yearly percent change, and the solid blue line is the average five-year percent change. The blue dashed lines are one standard deviation error bars.