Predicted habitat shifts of Pacific top predators in a changing climate

In this paper, we use state space modeled tracks from 15 species and previously identified relative density hotspots to examine predicted changes in habitat and top predator species richness under future climate scenarios. Detailed methods on number of animals tagged, weighting applied to tracks to deal with tag bias, and state space model fitting are included in Block et al. 2011 (supplemental methods 2.0-2.7, Table S3) and Winship et al. 2011. Figure 1 was re-created by integrating relative use as a function of the diversity of species visiting a cell, essentially a function of both the number of species that visit a cell and the number of individuals within a species that visit a cell. The TOPP species were chosen for this analysis based on a power analysis (1-β = 0.80, α = 0.05) in R (pwr package v. 1.1.1) to ensure sufficient sample sizes for the habitat modeling and predictions. We also scrutinized the spatial and temporal coverage of tag data to ensure that we were sampling a representative portion of the TOPP period in all four seasons (quarters) within the NE Pacific (10° to 60° N and 110° to 180° W). This resulted in a cutoff of 15 complete individual tracks per species (in line with Block et al. 2011). Species included are represented in Figure 4, while TOPP species that were not included were humpback whale (Megaptera novaeangliae), fin whale (Balaenoptera physalus), sperm whale (Physeter macrocephalus), northern fur seal (Callorhinus ursinus), thresher Shark (Alopias vulpinus), ocean sunfish (Mola mola), and Humboldt squid (Dosidicus gigas).

Generalized Additive Models (GAMs) were run iteratively in a model selection framework, building the models by running the relative use (number of times a grid cell was visited by a species) against environmental variables in the full model (sea surface temperature, chlorophyll-a, sea surface height anomaly, sea surface height root mean square, wind stress curl, latitude, longitude, and bottom depth) and then removing least significant parameters to get to a reduced model similarly to Block et al. 2011. Relative use only examined habitat grid cells visited by at least one individual per quarter allowing low, but non-zero use values. We examined the data for normality and cross-correlation using histograms, Q-Q plots, and correlation analyses. From these analyses, three link functions were explored, Gamma, Gaussian with log-transformed response data, and Poisson, and model fit and residuals were examined for normality. A Gaussian distribution with log-transformed species densities was chosen for the predictions as it resulted in the most normally distributed response variables and homogeneity in variance. Models were compared using AIC values and normality characteristics to determine the best-fit model. As SST and Chl were two key predictor variables across many of the species and were both available in the GFDL climate models, both were used in the species-specific generalized additive models. We have reported the p-values as part of the full model for each of these terms and the full and reduced model R² for each species (Table S1). Deviance explained by SST and Chl for each species was calculated by subtracting residual deviance from three models as described below:
(resid. deviance(SST) - resid. deviance(SST+CHL)) / resid. deviance(null model)

**Figure S1** Plots showing generalized additive model fit relationships between habitat, SST, and Chl by species for all 15 species. The habitat relative likelihood is on the y-axis with either SST (°C) or Chl (log10 mg/L) on the x-axis (indicated on right of plot).

Individual GAM plots for SST and Chl from the reduced model were used to examine species-specific responses for discussion in the manuscript (Figure S1). Core habitat was calculated by taking the top 25% of predicted habitat values from the GAM fits and then only including values above that threshold in future scenarios. The top 25% of habitat was chosen to ensure that we were focusing on the key habitat for each species and not modeling simply shortest-path migration corridors that may be less influenced by environmental features (similar to Kappes et al. 2010). We
recognize that finer scale analyses such as area-restricted search delineation to
examine actual behavioral characteristics (e.g. Bailey et al. 2010) could better
inform behavioral states (e.g. foraging versus migration), but this approach is better
suited for species-specific approaches to ensure we are not adding bias to the
biodiversity data. We lack data on prey resources and measures of foraging effort at
the appropriate scale for most of the species, and adding a proxy for foraging would
still remain a proxy and may confound inter-specific comparisons rather than
improve them. The numbers of species with core habitat in a cell for the quarter
were summed to calculate the metric of species richness.

![Figure S2](image)

**Figure S2.** Quarterly plots grouped by column of (a-d) SST (°C) and (e-h)
chlorophyll-\(a\) (mg/L) from 2001 to 2010 and changes in (i-l) SST and (m-p)
chlorophyll-\(a\) from the first and last two decades in the 21st century (2001 to 2020 &
2081 to 2100).

Climate predictions were calculated using a prototype earth system model (ESM
2.1) developed at NOAA’s Geophysical Fluid Dynamics Laboratory (GFDL). ESM 2.1
is a dynamic atmosphere-ocean general circulation model (Delworth et al. 2006)
coupled to a marine biogeochemistry model and has been used in a variety of recent
ecological studies of climate change in the North Pacific (e.g., Rykaczewski and
and divided by the baseline period (2001 to 2010) to get a measure of change in was subtracted from the mean number of cells from 2081 to 2100 for each species and divided by the baseline period (2001 to 2010) to examine spatial patterns of change (Figure S2).

Both sea surface temperature (from 0 to 10 meters) and chlorophyll-α (integrated from 0 to 100 meters) from the GFDL model output were averaged into a) monthly means from 2001 to 2100 and b) quarterly (seasonal) averages over 20-year windows to integrate across decadal variability and maximize the climate signal. Integrated chlorophyll-α matched the observed patterns in the north Pacific gyre better when compared to only surface Chl. Quarterly mean SST and Chl from 2001 to 2020 were subtracted from the quarterly means from 2081 to 2100 to examine areas of greatest change over the next century. Monthly predictions of SST and Chl were used in mgcv’s predict.gam to create the time series of species’ core habitat (Wood 2010).

Figure S3. Time series plots of core habitat changes (top 25% of all habitat) from 2001 to 2100 as monthly (gray), yearly (red) and 5-year (blue) predictions. 1 SD is shown in dashed blue lines.

The total numbers of cells in the species’ potential habitat were averaged across year and by quarter from 2001 to 2020. The quarterly climatology of core habitat was subtracted from the mean number of cells from 2081 to 2100 for each species and divided by the baseline period (2001 to 2010) to get a measure of change in
species richness (Figure 3). This process was repeated from 2001 to 2100 using monthly, yearly, and 5-year running mean values to examine how each species gained or lost habitat relative to the baseline period (Figure 4). The last year (2100) average minus the first year (2001) average was used to identify which species gained or lost habitat over the course of the simulation. Species-specific time series of habitat change are shown in Figure S3. The yearly average over the last 10 years and first 10 years from the modeled % core habitat were used to designate the predicted magnitude over the next century given that 2000-2010 was the “baseline” period of tagging effort (Figure 4F).

**Figure S4.** Plot of predicted relative habitat (from 1 = high to -1 = low) for test (25% of total) and training (75% of total) datasets. A linear model resulted in an R² value of 0.81.

To address the issue of model precision, we used a bootstrap approach randomly withholding 25% of the movement data from the entire modeling procedure: 1) final GAM fitting to 2) GAM predictions to 3) habitat change calculations. This approach allowed us both to a) test the models predicted relative use versus actual relative use values (Figure S4) and b) add standard deviation to our time series predictions to illustrate process variability (Figure 4, Figure S3). The 120 runs of test data (25%) were plotted against the training data (75%) and resulted in an R² of 0.81 indicating our models were successful in predicting relative use habitat from the predictor variables in the final model. The slope differed from 1 (1:1 line in dashed grey) suggesting that we over-predicted high values of relative use habitat. Given that we are using modeled values throughout the process and were focused only on the top 25% of habitat, this bias should not influence our percent-change calculations. The standard deviations were greatest for seabirds that had the
broadest distribution of habitat, and for turtles that had the fewest data points (Figure 4). Both of these guilds contained species with low GAM R² values (Table S1). All of the species trends save California sea lions were significantly different from zero using a 95% confidence level (1.96 * SD·n⁻¹/2).

This approach is not without caveats and the authors recognize that this is not intended to be a prediction of specific years with good or bad habitat nor a prediction of specific grid cells that a particular species will occupy in the future. Instead, this approach is a scenario-driven exercise to understand which species are most at risk of losing pelagic habitat in the future. Many tagged top predators use habitat beyond our study area but the study area had the greatest density of use for all 15 species (Block et al. 2011). Understanding ontogenetic shifts in habitat will be important given the relationship between body size to thermal physiology and migratory efficiency. Ultimately, we are modeling the realized niche rather than the actual niche such that climatic tolerances of species may be higher than they actually appear. In addition, we only used a single climate model realization for our predictions but it was the only model available with both SST and Chlorophyll-a data at the appropriate resolution (1°x1°). Broader analyses as more tag data are collected and additional climate simulations are available could refine our results in future modeling endeavors. Studies have examined the effects of sea surface temperature rise alone on marine species (e.g., Macleod 2009), however many top predators can easily move to avoid detrimental habitat and generalists can even switch prey if previous resources become inaccessible. Even given these caveats, these results are critical in understanding broad scale changes in top predator biodiversity, and identifying species that are at risk of losing pelagic habitat. Ideally, these results should be interpreted in the context of additional environmental and anthropogenic pressures in a cumulative framework to assess and adaptively manage these species at risk.
Table S1. SST and Chl deviance explained for each species from the reduced model. The full GAM and reduced GAM used for prediction $R^2$ values are included.

<table>
<thead>
<tr>
<th>Species name</th>
<th>SST dev</th>
<th>CHL dev</th>
<th>FULL GAM $R^2$</th>
<th>GAM $R^2$</th>
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<tr>
<td>Albacore tuna</td>
<td>5.26%</td>
<td>13.03%</td>
<td>34.30%</td>
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<td>Blackfoot albatross</td>
<td>4.25%</td>
<td>4.87%</td>
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<td>Bluefin tuna</td>
<td>18.43%</td>
<td>16.70%</td>
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<tr>
<td>Blue whale</td>
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<td>6.05%</td>
<td>24%</td>
<td>11%</td>
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<tr>
<td>California sea lion</td>
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<td>19.70%</td>
<td>17.10%</td>
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Mean values 27.50% 19.92%

Additional References


Wood, S. (2010). mgcv: GAMs with GCV/AIC/REML smoothness estimation and GAMMs by PQL. Available at http://cran.r-project.org/package=mgcv