

Predicted habitat shifts of Pacific top predators in a changing climate

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To manage marine ecosystems proactively, it is important to identify species at risk and habitats critical for conservation. Climate change scenarios have predicted an average sea surface temperature (SST) rise of 1–6 °C by 2100 (refs 1, 2), which could affect the distribution and habitat of many marine species. Here we examine top predator distribution and diversity in the light of climate change using a database of 4,300 electronic tags deployed on 23 marine species from the Tagging of Pacific Predators project, and output from a global climate model to 2100. On the basis of models of observed species distribution as a function of SST, chlorophyll *a* and bathymetry, we project changes in species-specific core habitat and basin-scale patterns of biodiversity. We predict up to a 35% change in core habitat for some species, significant differences in rates and patterns of habitat change across guilds, and a substantial northward displacement of biodiversity across the North Pacific. For already stressed species, increased migration times and loss of pelagic habitat could exacerbate population declines or inhibit recovery. The impending effects of climate change stress the urgency of adaptively managing ecosystems facing multiple threats.

Many top predators in marine ecosystems are in decline globally owing to overfishing, bycatch and other indirect anthropogenic threats including habitat loss and changes in prey availability³. Large ocean predators can provide top-down control of food webs and when these species are removed or displaced, resulting trophic cascades can alter the stability of marine ecosystems^{4,5}. Furthermore, changes in habitat may have multiple economic effects on coastal communities through reduced availability of ecosystem services such as fisheries landings and ecotourism.

Climate change has resulted in shifts in species distributions in both terrestrial and marine systems^{6,7}. Climate change ranks as one of the greatest anthropogenic threats to terrestrial biodiversity⁸, although less is known in marine systems. Models assessed by the Intergovernmental Panel on Climate Change estimate that global ocean surface temperatures will rise between 1 and 6 °C by 2100 (refs 1,2). Both acute and long-term exposure to warmer waters could impact species distributions through direct physiological and indirect ecological pathways^{9,10}. However, the rates and intensity of climate impacts will not be uniform across the world's oceans; thus,

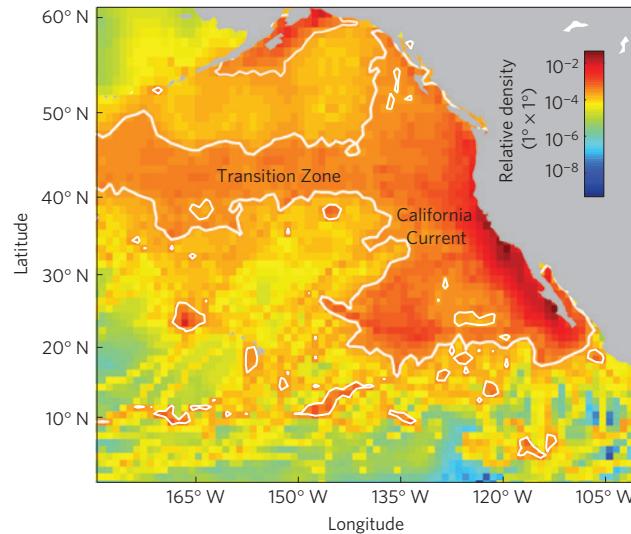


Figure 1 | Density of top predators within the eastern North Pacific.

Densities of the time-weighted and species-normalized position estimates of all tagged individuals were summed within 1° × 1° grid cells. The two densest biological hotspots are labelled; the white contour represents the top 25% of density values from 2001 to 2009. Modified from Fig. 4 of ref. 11.

understanding spatial patterns of change is critical for identifying ecosystems most at risk.

Comprehensive analyses of the effects of climate change inherently require an interdisciplinary approach. Remotely sensed environmental and animal distribution data can be combined in a habitat-modelling framework to both assess and predict how animals interact with their environment. The Tagging of Pacific Predators (TOPP) programme resulted in an unprecedented biologging data set by deploying over 4,300 electronic tags on 23 species from 2000 to 2009 in the North Pacific (Fig. 1). Pelagic predator hotspots in the northeast Pacific have been identified by quantifying the links between predator distribution and environmental features¹¹. Here we combine species-specific habitat models from the TOPP data set with climate change projections^{12,13} of SST and chlorophyll *a* to

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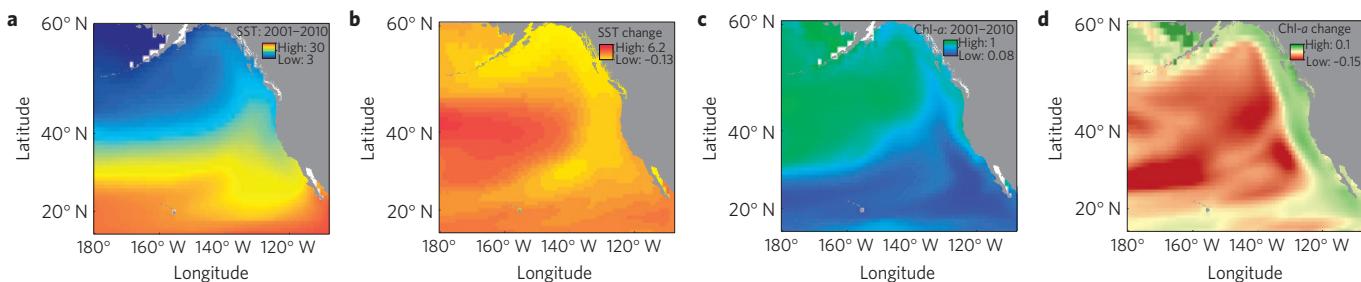


Figure 2 | Modelled SST and chlorophyll- α values and predicted changes. **a-d**, Yearly climatological maps of modelled SST and chlorophyll- α (Chl- α) patterns from 2001 to 2010 (**a,c**) and changes in SST and chlorophyll α from the first and last 20 years of 2001 to 2100 (**b,d**) in the North Pacific.

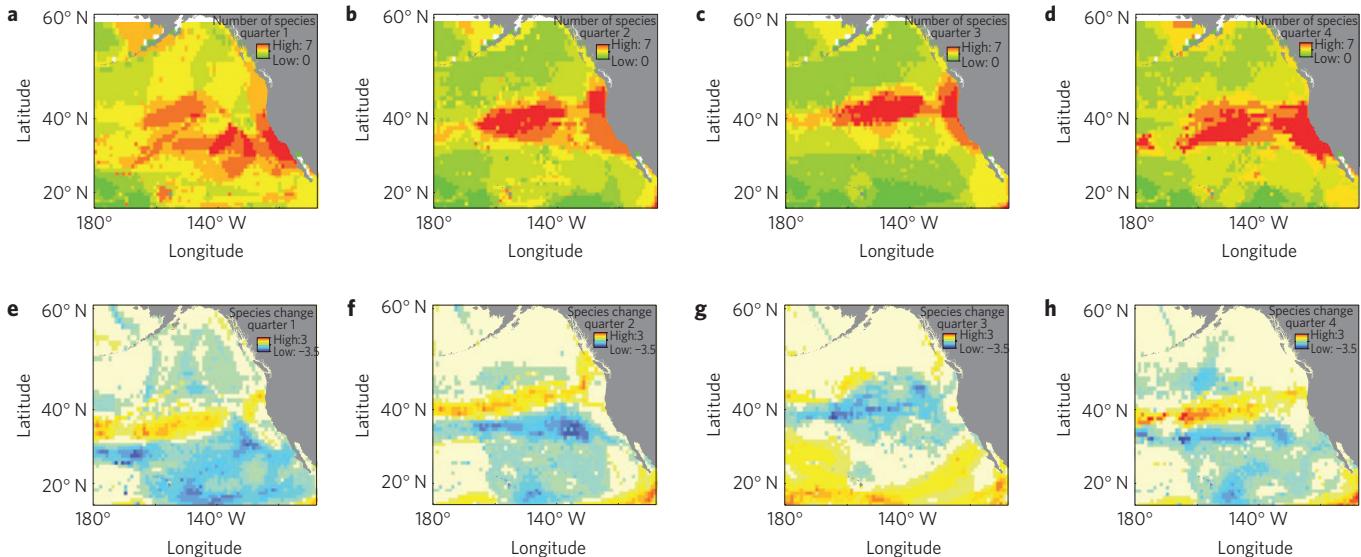


Figure 3 | Modelled species richness values and predicted changes. **a-h**, Quarterly modelled species richness for 2001–2010 from 15 top predator species (**a-d**) and predicted changes in species richness over the next century (2001–2020 compared with 2081–2100) (**e-h**).

predict rates and spatial patterns of change in top predator diversity, and species most at risk of losing pelagic habitat under climate change. This scenario-driven approach can be used to identify areas of stability as well as change in biodiversity across management boundaries, providing data essential to strategically and proactively manage dynamic marine ecosystems.

Results

The Geophysical Fluid Dynamics Laboratory coupled model for scenario A2 predicted SST changes as high as 5°C and chlorophyll- α changes up to $\pm 0.2 \text{ mg l}^{-1}$ between 2001 and 2100 in the northeast Pacific Ocean (Fig. 2). The largest temperature changes occurred in the North Pacific Transition Zone (NPTZ) whereas the upwelling-driven California Current Large Marine Ecosystem (CCLME) showed minimal change ($< 1^{\circ}\text{C}$). These trends were accompanied by a decrease in chlorophyll α in the central North Pacific and an increase in chlorophyll α along the coastal margins. Spatial patterns were similar under scenario A1B but had a lower magnitude of change (not shown).

We found varied relationships among core habitat and oceanographic variables across species. The mean deviance explained by the reduced generalized additive models was 20% for all species (minimum = 9% and maximum = 44%; Supplementary Table S1). The seabird guild targeted high-chlorophyll- α waters ($> 0.2 \text{ mg l}^{-1}$), the tuna guild targeted moderate SSTs ($\sim 15\text{--}25^{\circ}\text{C}$), whereas the shark guild targeted both higher chlorophyll α and moderate SST, highlighting the diversity of habitats used by top predators (Supplementary Fig. S1).

Predictive models of core habitat showed primary biodiversity hotspots in the CCLME and in the NPTZ ($\sim 43^{\circ}\text{N}$ latitude) with these regions serving as core habitat area for seven of the fifteen species during all seasons. These predicted results from 2001 to 2010 were similar to the previously published TOPP observations, validating our approach¹¹ (Fig. 1). Patterns in biodiversity showed a northward shift in core habitat as the NPTZ moved north in all seasons but the summer (Fig. 3). Richness decreased by up to 20% in the NPTZ and the warmer subtropical gyre as temperatures warmed in the winter, spring and autumn. Diversity patterns remained near constant in the California Current with the core habitat area of all species increasing 2% over the course of the twenty-first century.

There was high variability in predicted changes in core habitat area, $\pm 35\%$ across all species (Fig. 4 and Supplementary Fig. S3). Seabirds and tuna guilds had the greatest gains in potential core habitat, whereas the shark guild showed the greatest decline, and the marine mammal and turtle guilds had slight decreases. Rates of change were often nonlinear, with some species losing habitat quicker than others (Supplementary Fig. S3). Of all species, sooty shearwaters were predicted to have the greatest gain in habitat whereas mako sharks were predicted to lose the most habitat (Fig. 4f). Sooty shearwaters, blackfooted albatross and loggerhead turtles had the greatest variance in predicted habitat change.

Discussion

We used spatial models of top predator species distributions in concert with global climate models to project changes in North Pacific biodiversity hotspots and to identify functional groups

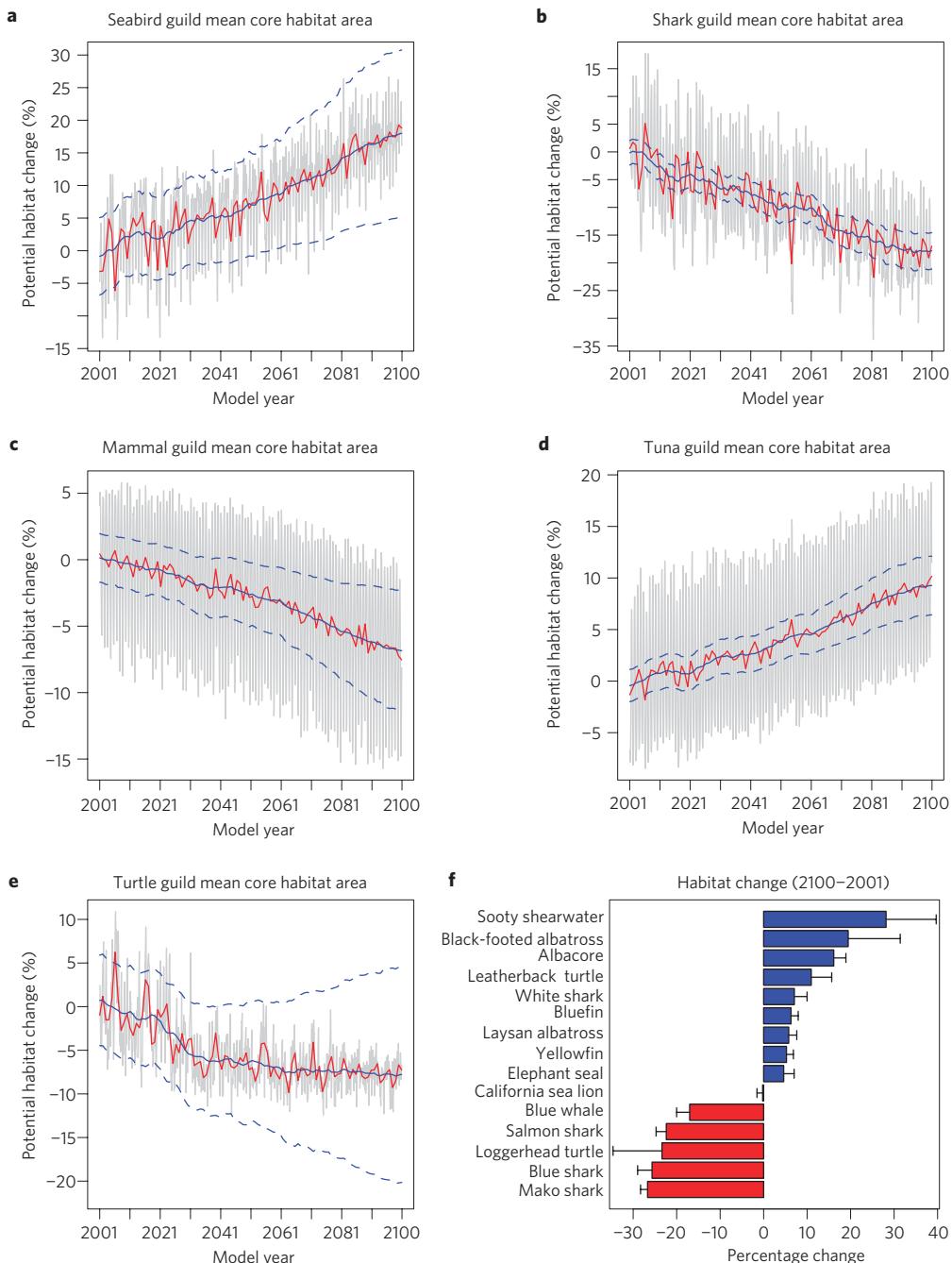


Figure 4 | Predicted changes in top predator core habitat by guild. **a–e**, Top predator core habitat area by guild from 2000 to 2100 shown as monthly (grey), yearly (red) and 5-year filtered (blue) time series with 1 standard deviation marked by dashed lines. **f**, Total predicted mean habitat change from 2001 to 2100 for each of the 15 top predator species with 1 standard deviation error bars.

most at risk. The climate model output showed a northward migration of up to 1,000 km of the NPTZ, contraction of the subarctic gyre and expansion of the oligotrophic subtropical gyre¹⁴ (Fig. 2). These physical changes will drive a substantial northward shift in biodiversity across the North Pacific for species with both commercial and conservation value. Modelled ecosystem changes predict increased species overlap and a potential for niche compression under the Intergovernmental Panel on Climate Change A2 scenario (Fig. 3).

We found significant differences in habitat change across guilds resulting in species-specific winners and losers. The shark guild showed the greatest risk of pelagic habitat loss with 3 out of 4 species showing declines (Fig. 4 and Supplementary Fig. S3). Tuna species

gained core habitat, potentially owing to their higher use of the CCLME. Marine mammals declined in potential habitat, largely driven by blue whales, whereas seabirds had the greatest increase in potential habitat. Species with specialized diets (for example, blue whales and leatherbacks) may have less capacity for adaptation and therefore will be more susceptible to environmental changes than prey-switching generalists (for example, tuna and seabirds)^{10,15}. Similarly, species with broader thermal tolerances may be more successful than those with limited thermal tolerances⁶. In addition, increases in fisheries catch may exacerbate climate change effects on both fished species and predator populations^{15–17}.

Our predicted climate change impacts on threatened or endangered species could have varied effects on population recovery

efforts. Marine top predators can have high phenotypic plasticity and adaptive capability that may reduce climate change impacts, whereas mismatches between predators and prey due to climatic shifts could enhance climate change impacts. Among turtles, loggerheads showed a decline in core habitat, whereas leatherbacks foraging in the California Current had a slight increase in potential habitat projected. However, nesting beach development and skewed sex ratios from warmer nesting temperatures may negate projected foraging habitat gains for endangered leatherbacks¹⁸. Seabirds had the greatest predicted gains in pelagic habitat, but changes in wind regimes and resultant migration corridors may mean potential habitat is inaccessible¹⁹. Furthermore, loss of seabird nesting habitat on low-lying atolls due to sea-level rise may lead to population extinctions²⁰. Blue whales showed a decrease in predicted core habitat, which could limit their post-whaling recovery²¹, whereas elephant seals were predicted to have an increase in available habitat in the North Pacific. Central place foragers such as pinnipeds and seabirds have additional constraints when compared with migratory fish, sharks and whales, as hotspots such as the NPTZ may move further from existing colonies, adding increased energetic cost and decreasing reproductive success, particularly during sensitive life-history stages¹⁹ (Fig. 3).

Waters within the west coast US exclusive economic zone were predicted to increase in chlorophyll *a* and also remain high biodiversity hotspots in the future (Figs 2 and 3). As offshore habitat decreases or becomes less accessible, there may be increased use in the CCLME leading to greater competition among top predators, but also a higher risk of anthropogenic impacts such as shipping traffic and fisheries bycatch²². In the Pacific, oxygen minimum zones are both expanding and shoaling²³. A shallower oxygen minimum zone could reduce vertical habitat for fishes with high oxygen demand while concentrating prey for air-breathing mammals, turtles and seabirds. In a spatially explicit framework, maps of changes in ecosystem services, habitat preferences and trophic interactions could serve as the foundation for reserve design and marine spatial planning in a changing ocean²⁴.

The complexity and broad-scale effects of climate change make it difficult to determine changes or distributional shifts *a priori*. Marine organisms, particularly pelagic predators, offer added difficulty in prediction because they are highly migratory, spend a large portion of their lives below the surface of the ocean and have complex physiological specializations¹¹. However, the marine realm is predicted to face marked changes by 2040 (ref. 25), so we must use our best science to identify individual species and biodiversity hotspots most at risk and to implement management and intervention methods using a precautionary approach²⁶. Habitat models based on animal movement data and real-time oceanography open the possibility of dynamic marine protected areas that are oriented to transient oceanic features (for example, fronts, eddies and upwelling zones) rather than those fixed on stationary habitats (for example, reefs and seamounts). Policy prescriptions for pelagic marine reserves are being actively debated now both inside exclusive economic zones of nations and in the open sea²⁷. Management strategies and reserves need to be based not only on present biodiversity distributions and migration corridors but also on their persistence in the future.

To truly understand the multiple stressors faced by a species, an ecosystem-based approach is needed. Integrated ecosystem models of trophic dynamics and energy flow could be used to look at changes in forage species and the effects on predators²⁸ in addition to predicted changes in fisheries landings¹⁷. These modelling approaches are not without limitation, as a 1° grid-size model does not resolve fine-scale oceanic or ecological processes that interact on the scale of individuals¹³. Results of this and similar approaches^{29,30} are critical to initially assess risk and vulnerability of species to climate change so that managers can proactively target

those species most at risk. Climate change is a broad-scale and directional process and we must plan accordingly to ensure our healthy and functioning ecosystems remain intact, and recovery efforts are appropriately targeted and successful.

Methods

Fifteen of the twenty-three TOPP species had sample sizes sufficient to use in our analysis (resulting in 1791 individual tracks, see Supplementary Information). We used a Bayesian state-space model to account for variable levels of observation error among tag types and to produce regular daily location positions including estimates of uncertainty¹¹. Tracks were normalized by deployment duration to account for tag biases¹¹. We modelled the density of each predator species in 1° × 1° grid cells as additive, non-parametric functions of oceanographic variables, bathymetry and season. Satellite-derived fields of chlorophyll *a*, SST, sea surface height anomaly and variance, wind stress curl and bathymetry were used to create time series of monthly values within each grid cell from 2000 to 2009. We fitted generalized additive models for species densities within each grid cell in a full model (all environmental variables) and subsequently in a reduced model for chlorophyll *a*, SST, latitude, longitude and bathymetry.

We used output from a prototype Earth system model (ESM2.1) developed at the Geophysical Fluid Dynamics Laboratory of the National Oceanic and Atmospheric Administration (NOAA). ESM2.1 is a dynamic atmosphere–ocean general circulation model¹² coupled to a marine biogeochemistry model that allows us to project spatial patterns in SST and chlorophyll *a* (refs 13,14). Whereas most climate change models use SST alone, we examined monthly changes in both SST and chlorophyll *a* from 2001 to 2100, which informed our generalized additive model predictions for each species. ESM2.1 was not initialized to observations; thus, decadal variability is represented statistically but the phase of variability will not match observed phases.

We modelled changes in the 15 species distributions from 2001 to 2100 and used 120 bootstrapped runs to examine process variability. Core habitat was defined as the upper 25th percentile of habitat use based on SST, chlorophyll *a* and bathymetry thresholds from model fits (see Supplementary Information). Spatial changes in patterns of biodiversity were examined using species richness indices by summing the number of species with core habitat in each grid cell. Mean richness from 2001 to 2020 was compared with richness from 2081 to 2100 to examine the climate change signal independent of decadal variability.

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Author contributions

This climate modelling study was initiated by E.L.H., S.J.B., S.J.J. and R.R.R. The TOPP project was designed and data collection was coordinated by B.A.B., D.P.C. and S.J.B. Tracking data for this project were compiled by S.J.J. and I.D.J., and climate model data were compiled by R.R.R. and J.P.D. Oceanographic data were compiled by E.L.H., S.J.B. and D.G.F. Analyses were conducted by E.L.H., S.J.J., S.J.B. and R.R.R. Figures were created by E.L.H., S.J.B., D.G.F. and S.J.J. The manuscript was written by E.L.H. and edited by S.J.J., R.R.R., S.J.B., D.G.F., I.D.J., S.A.S., L.B.C., J.P.D., D.P.C. and B.A.B.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to E.L.H.

Competing financial interests

The authors declare no competing financial interests.

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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 ($1-\beta = 0.80$, $\alpha = 0.05$) 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 R^2 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:

$$(resid. deviance(SST) - resid. deviance(SST+CHL)) / resid. deviance(null model)$$

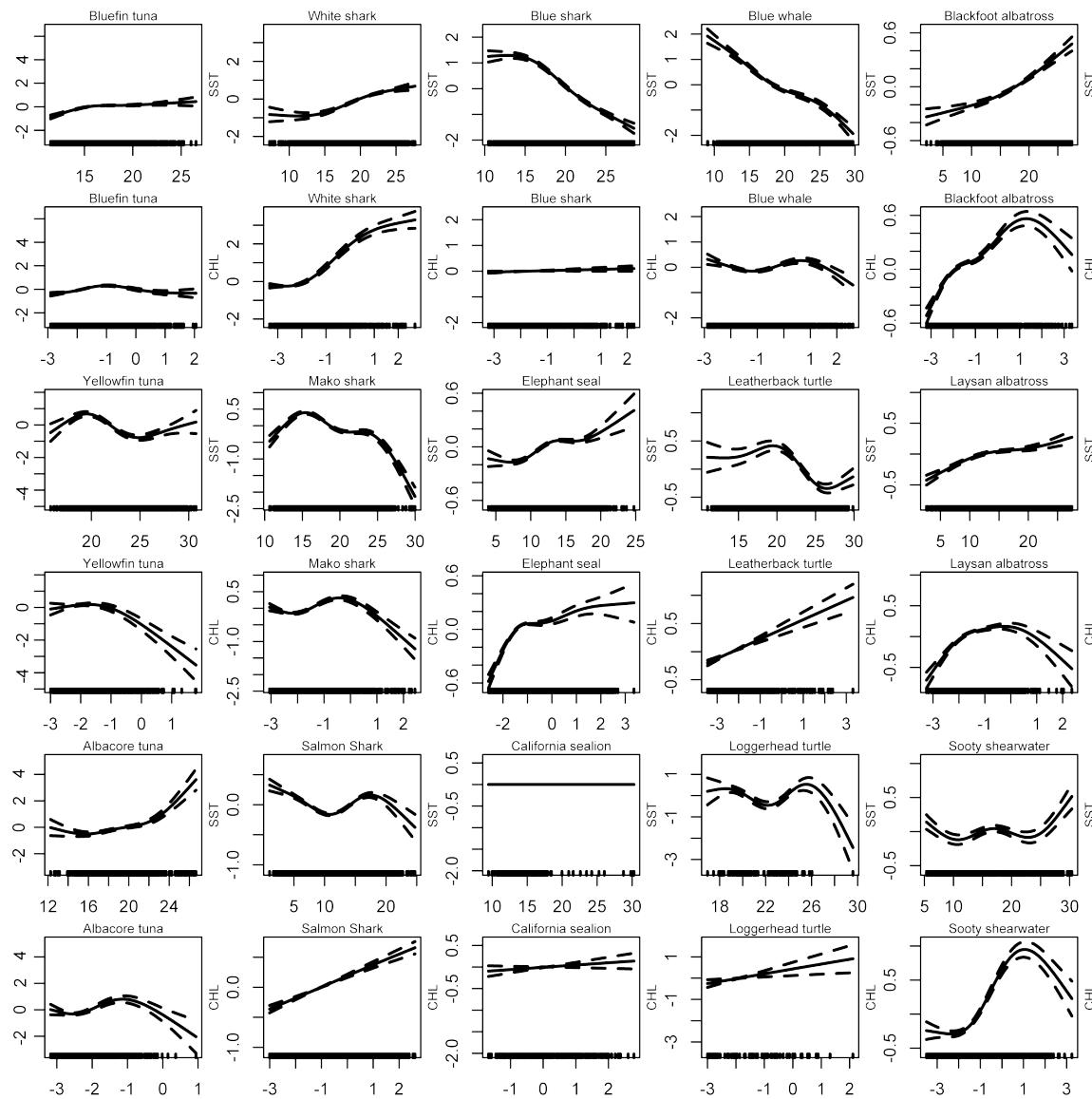


Figure S1 Plots showing generalized additive model fit relationships between habitat, SST, and Chl by species for all 15 species. The habitat relative likelihood is on the y-axis with either SST ($^{\circ}\text{C}$) or Chl ($\log_{10} \text{mg/L}$) on the x-axis (indicated on right of plot).

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.

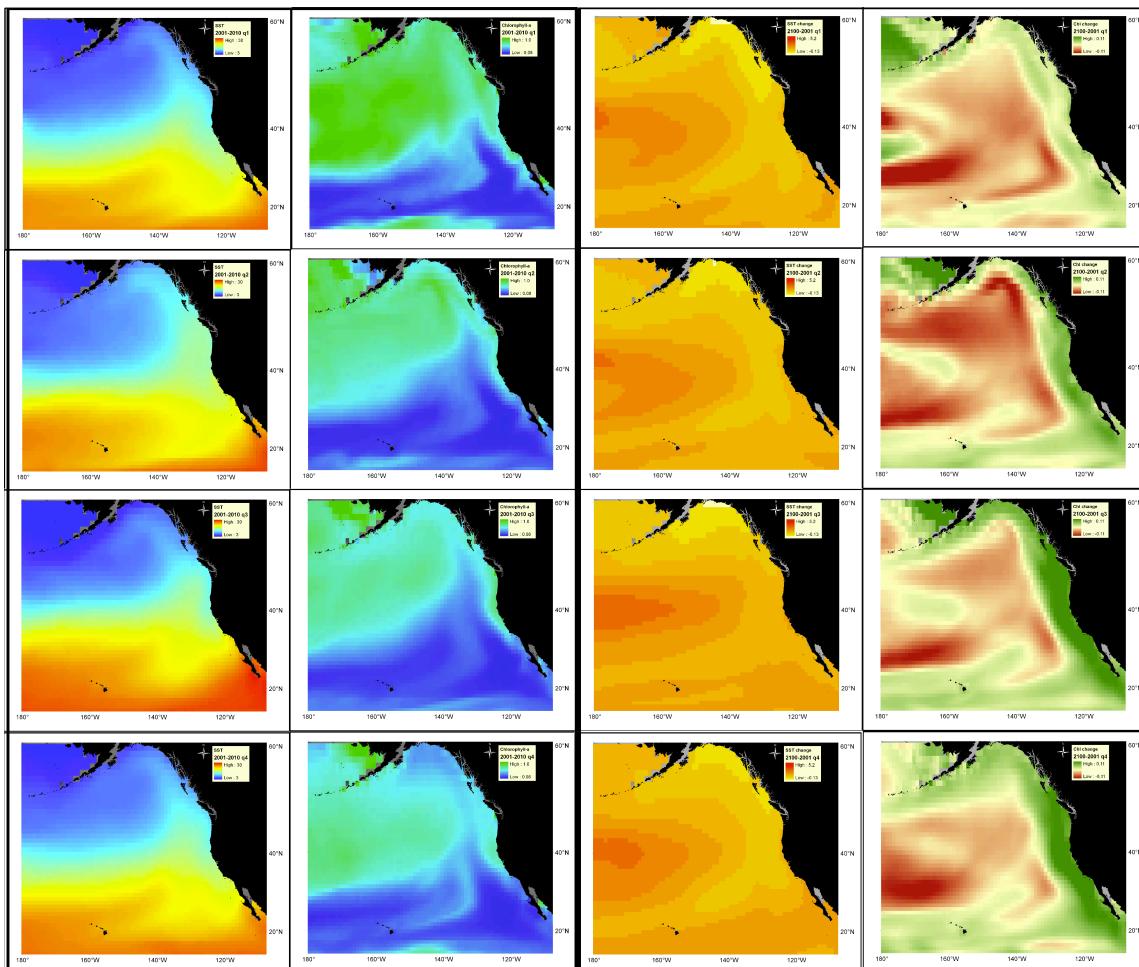


Figure S2. Quarterly plots grouped by column of (a-d) SST ($^{\circ}\text{C}$) and (e-h) chlorophyll-*a* (mg/L) from 2001 to 2010 and changes in (i-l) SST and (m-p) chlorophyll-*a* from the first and last two decades in the 21st century (2001 to 2020 & 2081 to 2100).

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

Dunne 2010, Polovina et al. 2011). Most of the global climate models do not include predictions of chlorophyll-*a*, which was critical to our analysis. We chose the A1B and A2 scenarios as these predicted more extreme greenhouse gas emissions over the next century of 720 ppm and 840 ppm respectively (IPCC 2007). The A1B scenario assumes rapid growth through 2050 with an ultimate switch to cleaner technologies, while the A2 scenario is termed “business as usual” and assumes a near constant increase in greenhouse gas emissions. Quarterly predictions were made from 2001 to 2100, and the predictions from 2001 to 2020 were subtracted from 2081 to 2100 to examine spatial patterns of change (Figure S2).

Both sea surface temperature (from 0 to 10 meters) and chlorophyll-*a* (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-*a* 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).

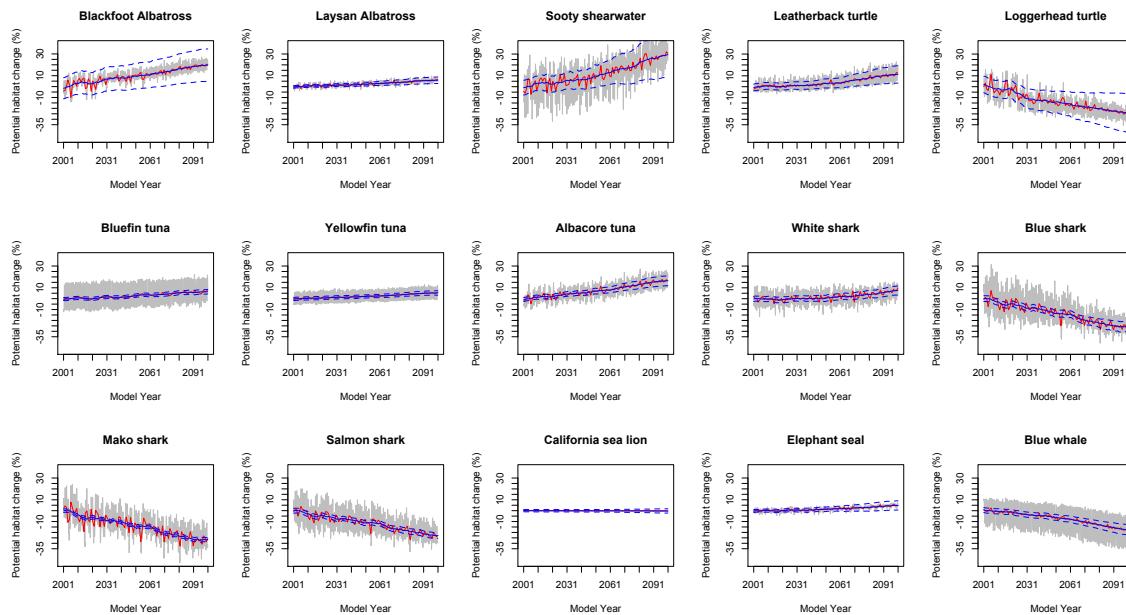
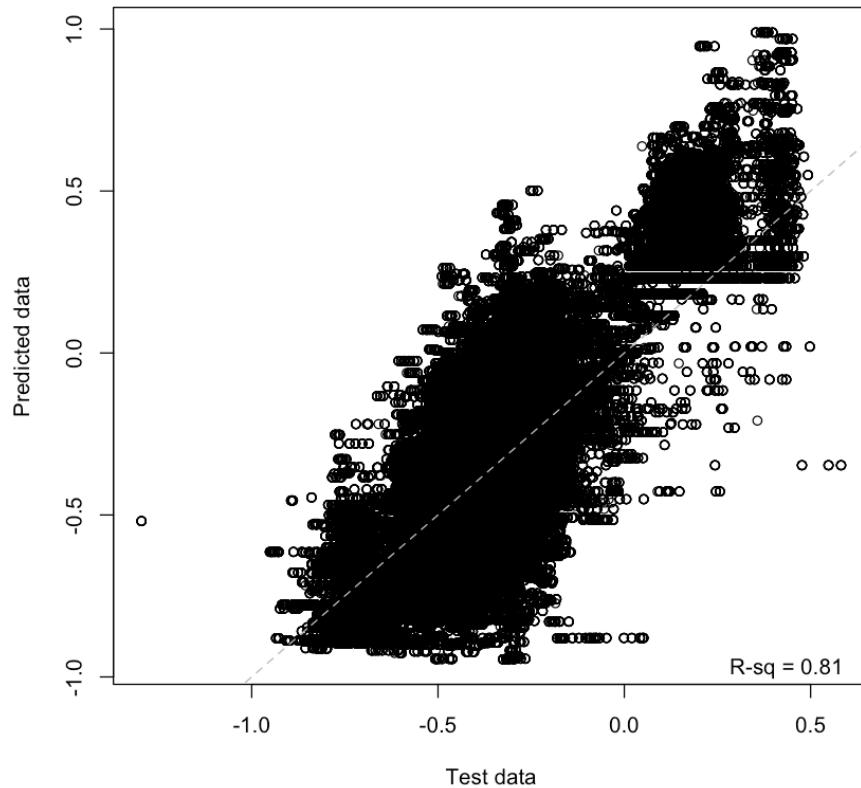


Figure S3. Time series plots of core habitat changes (top 25% of all habitat) from 2001 to 2100 as monthly (grey), yearly (red) and 5-year (blue) predictions. 1 SD is shown in dashed blue lines.

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 R^2 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 R^2 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 ($1.96 * \text{SD} \cdot n^{-1/2}$).

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 R² values are included.

Species name	SST dev	CHL dev	FULL GAM R ²	GAM R ²
Albacore tuna	5.26%	13.03%	34.30%	29.70%
Blackfoot albatross	4.25%	4.87%	9.64%	9.51%
Bluefin tuna	18.43%	16.70%	51.20%	43.80%
Blue shark	2.07%	1.80%	23.40%	13.60%
Blue whale	2.87%	6.05%	24%	11%
California sea lion	4.23%	14.53%	33.00%	22.70%
Elephant seal	3.36%	2.18%	13.50%	8.60%
Laysan albatross	1.53%	2.69%	11.40%	9.30%
Leatherback turtle	1.29%	0.85%	23.10%	9.53%
Loggerhead turtle	12.25%	9.47%	50.30%	35.30%
Mako shark	3.81%	6.77%	24.40%	24.20%
Salmon shark	2.25%	11.45%	20.40%	13.80%
Sooty shearwater	3.87%	16.76%	42%	34%
White shark	3.83%	13.66%	32.80%	16.70%
Yellowfin tuna	3.63%	8.67%	19.70%	17.10%
Mean values			27.50%	19.92%

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