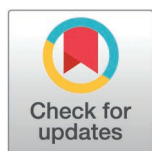


RESEARCH ARTICLE

Projected changes to the extent and seasonality of seabird habitat in the California current and implications for marine spatial planning

Ryan Gasbarro^{1*}, David G. Ainley², Kelly S. Andrews³, Lisa T. Ballance⁴, Hannah Blondin^{5,6}, Steven Bograd⁷, Stephanie Brodie⁸, Megan Cimino⁹, Thomas Clay^{1,9}, Aspen Ellis¹⁰, Joseph Evenson¹¹, John C. Field¹², Elliott L. Hazen⁷, Michael Jacox⁷, Jaime Jahncke¹³, Trevor Joyce¹⁴, Jeffery B. Leirness^{15,16}, Danielle Lipski¹⁷, Barbara Muhling¹, Nerea Lezama-Ochoa¹, Mercedes Pozo Buil¹, Adena Schonfeld¹, Amanda Warlick^{1,3}, Heather Welch¹, Jen Zamon¹⁸, Kelly M. Zilliacus¹⁰, Jarrod A. Santora¹²



OPEN ACCESS

Citation: Gasbarro R, Ainley DG, Andrews KS, Ballance LT, Blondin H, Bograd S, et al. (2025) Projected changes to the extent and seasonality of seabird habitat in the California current and implications for marine spatial planning. PLOS Clim 4(11): e0000687. <https://doi.org/10.1371/journal.pclm.0000687>

Editor: Johanna E Johnson, James Cook University, AUSTRALIA

Received: July 1, 2025

Accepted: October 15, 2025

Published: November 10, 2025

Copyright: This is an open access article, free of all copyright, and may be freely reproduced, distributed, transmitted, modified, built upon, or otherwise used by anyone for any lawful purpose. The work is made available under the [Creative Commons CC0](https://creativecommons.org/licenses/by/4.0/) public domain dedication.

Data availability statement: R code and data used for analyses and figures is available at: <https://doi.org/10.5281/zenodo.17145095> and <https://doi.org/10.5281/zenodo.17145108>. Historical environmental data from the ROMS

1 Institute of Marine Science, University of California, Santa Cruz, Santa Cruz, California, United States of America, **2** H.T. Harvey & Associates, Los Gatos, California, United States of America, **3** Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington, United States of America, **4** Marine Mammal Institute, Oregon State University, Newport, Oregon, United States of America, **5** Marine Mammal and Turtle Division, Southeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Miami, Florida, United States of America, **6** Cooperative Institute of Marine and Atmospheric Studies, University of Miami, Miami, Florida, United States of America, **7** Ecosystem Science Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Monterey California, United States of America, **8** Environment Research Unit, Commonwealth Scientific and Industrial Research Organisation, Brisbane, Australia, **9** People and Nature, Environmental Defense Fund, Monterey, California, United States of America, **10** Conservation Action Lab, University of California, Santa Cruz, California, United States of America, **11** Washington Department of Fish and Wildlife, Olympia, Washington, United States of America, **12** Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Santa Cruz, California, United States of America, **13** Point Blue Conservation Science, Petaluma, California, United States of America, **14** Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, California, United States of America, **15** CSS Inc., Fairfax, Virginia, United States of America, **16** National Centers for Coastal Ocean Science, National Oceanic and Atmospheric Administration, Silver Spring, Maryland, United States of America, **17** Cordell Bank National Marine Sanctuary, National Oceanic and Atmospheric Administration Office of National Marine Sanctuaries, Point Reyes Station, California, United States of America, **18** Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Point Adams Research Station, Hammond, Oregon, United States of America

* rygasbar@ucsc.edu

Abstract

Climate-induced changes in ocean conditions are likely to affect species habitat use across current management boundaries (e.g., marine protected areas). Therefore, it is important to identify potential future risks that may reduce the effectiveness of fixed boundaries or cause negative interactions between wildlife and human ocean-use sectors. Here, we used presence and absence records from a compilation of > 132,000 ship-based and aerial at-sea visual survey transect segments collected from 1980–2017 to fit species distribution models (SDMs) for five abundant and

re-analysis are available at oceanmodeling.ucsc.edu. Monthly downscaled climate projections are available online at: <https://oceanview.pfeg.noaa.gov/erddap/search/index.html?searchFor=ccs+roms>. Seabird survey data combined across all surveys is summarized in this report: <https://pubs.usgs.gov/publication/70228321>. Monthly aggregated SDM projections from 1980–2100 are available on ERDDAP: <https://oceanview.pfeg.noaa.gov/erddap/files/SeabirdsProjection/>. Raw seabird survey data is confidential and can be acquired by direct request from data holders, subject to a non-disclosure agreement. Seabird surveys have a number of lead contacts, and some of those contacts are listed below. Further information on how to obtain additional data can be directed to R. Gasbarro (rygasbar@ucsc.edu). For ACCESS surveys, contact J. Jahncke (jjahncke@pointblue.org). For CalCurCEAS, CSCAPE, and ORCAWALE, contact L.T. Ballance (lisa.ballance@oregonstate.edu). For EPOCS & Pelagic Juvenile Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) contact D. Ainley (dainley@harveyecology.com) and Jarrod Santora (jarrod.santora@noaa.gov); RREAS seabird data from 1996–2021 are publicly available at https://oceanview.pfeg.noaa.gov/erddap/tabledap/RREAS_FI_SBAS_obs.html. For updated seabird data for JSOES and PODS contact J. Zamon (jen.zamon@noaa.gov). For Pacific Coast Winter Sea Duck Survey, contact J. Evenson (joseph.evenson@dfw.wa.gov). CalCOFI data are available at <https://calcofi.org/data/marine-ecosystem-data/seabirds/>. Additional data are available from the North Pacific Pelagic Seabird Database (ver. 4.1): <https://doi.org/10.5066/F7WQ01T3>.

Funding: This work was funded by NOAA's OAR Climate Program Office (NA22OAR4310560), and with temporary funding from NOAA's Integrated Ecosystem Assessment (IEA) Program (RG) and an Interagency Agreement between the U.S. Department of the Interior, Bureau of Ocean Energy Management and the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center (M24PG00004 to KSA). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. The findings and conclusions in the paper are

ecologically important seabird species in the California Current Ecosystem (CCE), including both resident (common murre, Cassin's auklet, and rhinoceros auklet) and seasonal migrant (sooty shearwater, black-footed albatross) species with different life-histories. We then projected their daily habitat suitability from 1980–2100 using an ensemble of three dynamically downscaled, high-resolution (0.1°) climate projections for the CCE. We compared long-term changes in both mean conditions and intra-annual (seasonal) variability within four National Marine Sanctuaries and four proposed areas for offshore wind energy development in the CCE. Sea surface temperature, bottom depth, daylength, and biogeographic province were the most important variables, with relative importance being species-specific. Each species displayed a negative relationship with increasing temperatures that was most pronounced in the two auklet species. Accordingly, habitat suitability scores declined across the CCE, most prominently south of Point Conception, emerging from historical variability for all species except sooty shearwater. Despite long-term negative trends in habitat suitability, we identified extensive species-specific seasonal refugia, highlighting potential changes in the intra-annual occurrence of suitable habitat. Our results suggest that perceptions of conservation benefits of marine sanctuaries and potential interactions between seabirds and new ocean-use development could be notably different by 2100, and that many impacts may occur by mid-century. Thus, it is critical to consider future projections of species habitat suitability within marine spatial management and planning processes.

Introduction

Climate-induced changes in ocean conditions, including warming, deoxygenation, acidification, and changes in primary productivity, are reshaping marine ecosystems globally, and altering the effects of direct anthropogenic stressors, such as fishery depletion and resource development [1–6]. Climate stressors can affect species' distributions directly via physiological responses or indirectly via modifications to habitats or food webs [7–9]. Range shifts or behavioral changes linked to environmental conditions (e.g., prey-switching, migratory patterns) may lead to mismatches in phenology and predator/prey overlap, or increased species overlap as available suitable habitats are compressed into smaller areas [10–12]. There are a number of factors influencing the severity of climate-associated impacts on species' distributions, including local rates of environmental changes, species niche breadths, and phenological/behavioral flexibility [13,14]. Syntheses of observational datasets at the scale of large marine ecosystems and robust comparisons between species will help resolve the relative importance of these factors, improve baseline information of species habitat suitability, and identify important habitats that may be susceptible to change.

Despite the dynamic nature of species distributions and climate variability, management actions are generally applied within spatially-fixed boundaries, such as

those of the authors and do not necessarily represent the views of NOAA and the National Marine Fisheries Service or external funding partners.

Competing interests: The authors have declared that no competing interests exist.

geopolitical boundaries or area-based conservation measures such as Marine Protected Areas [MPAs; [15,16](#)]. It is important to understand how species habitat use may change across current management boundaries and identify potential future risks that reduce effectiveness of fixed boundaries [[17–20](#)] or cause negative interactions between wildlife and human ocean-use sectors (e.g., offshore wind energy development areas; [[21](#)]). Seabirds are of particular concern because they move freely in and out of management boundaries, which increases the likelihood of interactions with static infrastructure (e.g., offshore wind farms) that may displace foraging habitat or cause macro-avoidance behaviors [[22–26](#)] that affect their distributions. Therefore, assessing environmental determinants and uncertainty of seabird ocean habitat suitability can offer insights into ocean-modulated processes that may affect the future efficacy of marine spatial planning [[27,28](#)].

Seabirds are highly mobile taxa that live at the interface of air and ocean with an array of life history (e.g., reproductive strategy) and behavioral (e.g., flight and foraging patterns) traits [[29–31](#)]. Seabirds are considered ocean-climate and ecosystem sentinels due to their sensitivity to environmental and resource variability [Pichegeru et al. 2010; [32–34](#)]. Generally, seabird foraging and reproductive ecology falls into two behavior categories: central place foraging by residents, and long-distance travels to seasonally available foraging locations [[30](#)]. In the California Current Ecosystem (CCE), trans-hemisphere migrants (e.g., sooty shearwater) may modify the timing of migration or the time spent in intermediate habitats under variable conditions ([[35,36](#)]). Resident species' distributions are tied to local physiographic features, and may thus compress towards the coast due to decreases in offshore prey availability associated with ocean warming [[11,37,38](#)]. The utility and response of seabird ecosystem indicators (e.g., foraging and reproductive ecology and behavior) may be manifested by changes in the availability of suitable ocean habitat, which reflects both environmental preferences and the spatiotemporal arrangement of prey resources [[39,40](#)]. Climate-associated alterations in food webs have affected seabirds' reproductive timing, productivity, and at-sea distributions [[41–43](#)]. Additionally, acute events, such as marine heatwaves, have been associated with starvation and mass stranding events of Cassin's auklets and common murrelets in the North Pacific [[44–46](#)], while several booby species have expanded their ranges northward in the region in response to more frequent marine heatwaves and altered ocean climate [[47](#)].

Applied future climate projections from earth system models to species distribution models (SDMs) may inform spatial protections and strategic siting of anthropogenic activities to minimize wildlife interactions (e.g., [[27,48,49](#)]). Projected indices of habitat suitability may be used to develop baselines and identify areas where future conditions are within the bounds of species' historical climate envelope (i.e., climate refugia), as well as areas that may become more or less suitable, to contribute to marine spatial planning [[19,28,49,50](#)]. While several studies have projected seabird habitat into the future under different climate change scenarios (e.g., [[51–55](#)]), few have considered future redistributions within the context of marine spatial planning, including both MPAs and anthropogenic infrastructures. There are also no projections

of climate impacts on seabird ocean habitat within the CCE, one of the most productive and diverse seabird regions in the world [56,57]. The CCE also supports diverse anthropogenic activities such as commercial fishing and energy development [58,59], including four proposed areas for offshore wind energy development (Wind Energy Areas; WEAs). In addition, a number of management areas occur in the CCE, perhaps the most notable among them are the network of National Marine Sanctuaries (NMS). It is currently unknown to what extent the static boundaries of NMS and WEAs in the CCE (Fig 1) will remain relevant for seabird conservation and protected species management in the future.

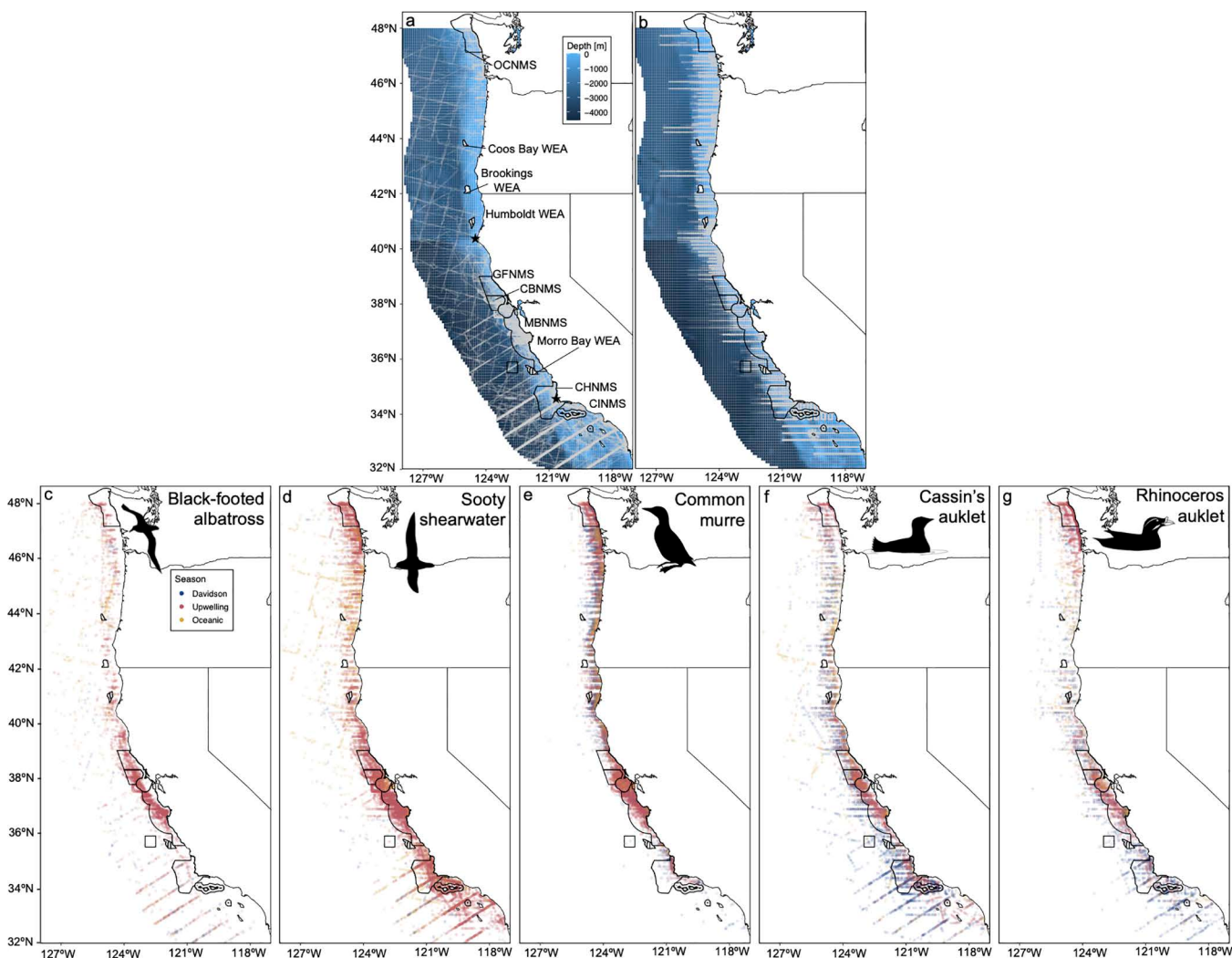


Fig 1. Maps of study area and occurrence data used to build SDMs. (a) Ship-based and (b) aerial survey locations (gray points) within the 273 km boundary covered by both survey types with bathymetry (colors) overlain. Biogeographic boundaries at Cape Mendocino and Point Conception are denoted with stars, and both National Marine Sanctuary (clear polygons) and offshore Wind Energy Area (white polygons) boundaries are shown. (c-g) Species occurrences by season (symbol color); see S1 Fig A S1 Text for maps of all aerial- and ship-based survey presences and absences outside of the 273km shore-distance contour. CBNMS=Cordell Bank National Marine Sanctuary; CINMS=Channel Islands National Marine Sanctuary; CHNMS=Chumash Heritage National Marine Sanctuary; GFNMS=Greater Farallones National Marine Sanctuary; MBNMS=Monterey Bay National Marine Sanctuary OCNMS=Olympic Coast National Marine Sanctuary. Note that CINMS and OCNMS are not included in analyses (see Methods) but are shown in maps for reference.

<https://doi.org/10.1371/journal.pclm.0000687.g001>

Here, using a long-term dataset of species presence-absence covering the entirety of the CCE, we develop and evaluate SDMs of habitat suitability for five seabird species, including both resident and seasonal migrant species with different life-histories (e.g., alcids, procellariids). We then project their daily habitat suitability from 1980 to 2100 using an ensemble of dynamically downscaled climate projections for the CCE [60]. Our first objective is to evaluate species-specific responses to ocean variables, and the relative importance of these variables in explaining habitat suitability for each species. We then quantify and map the spatial extent and suitability of historical and future seabird habitat. We assess long-term changes in both mean conditions and intra-annual (seasonal) variability within four NMS and four proposed areas for offshore wind energy development (WEAs) in the CCE (Fig 1). These assessments occur within boundaries of conservation and management importance, and allow us to compare the magnitude and seasonality of projected changes across the biogeographic provinces, cross shelf gradients, and latitudinal range of the CCE [61–64]. By comparing model projections across multiple species and earth system models, we examine the implications of changing seabird habitat for marine spatial planning throughout the CCE, and illustrate how the perceived benefits (e.g., conservation gains from NMS) and conflicts (e.g., habitat displacement from WEAs) arising from static management boundaries may change when changes in ocean climate are considered.

Materials and methods

Study setting

The CCE is an eastern boundary upwelling system extending from Baja California, Mexico (~27° N) to the North Pacific Transition Zone (~50° N) [62]. Ecosystem conditions vary between three oceanographic seasons (i.e., Davidson Current, Upwelling & Oceanic), with distinct effects on the distribution of marine biota [61,65]. There are a number of fixed management areas in the CCE, including a network of NMS (Fig 1). These sanctuaries were established to safeguard both natural and human heritage resources in the CCE [66]. A number of highly mobile pelagic species of ecological and conservation importance (e.g., protected species) occur seasonally within these NMS for diverse habitat uses including feeding and reproduction [67]. Seabirds have played a particularly important role in the NMS system since their inception. Colony locations were important information used in the designation of some NMS in light of, e.g., emergent oil spill risks [68–70]. Seabird abundance and diversity have also been proposed as quantitative ecological indicators of sanctuary condition [71]. NMS contain seabird assemblages with elevated levels of both metrics compared to surrounding areas [35, Santora et al. 2021; 63], and also feature in some sanctuary management plans (e.g., [72,73]). We included four of the six CCE NMS in our analyses: Chumash Heritage, Monterey Bay, Greater Farallones, and Cordell Bank (Fig 1). Olympic Coast NMS - the northernmost NMS and a hotspot for seabird prevalence located in Washington State off the Olympic Peninsula (Table 1) - was excluded because it falls predominantly outside of the model domain. Channel Islands NMS was also excluded due to the relatively low prevalence or complete absence of our focal species (Table 1), and the small coastal domain that is challenging to compare with other NMS that extend continuously from the coast to the continental slope.

Offshore wind energy is a burgeoning new ocean-use sector within the CCE. The proposed development of offshore wind energy in the U.S. West Coast utilizes floating-platform technology, anchored to the seabed with transmission cables suspended in the water column in areas with depths exceeding 60 m along the continental shelf [74]. The U.S. Department of Interior's Bureau of Ocean Energy Management (BOEM) is responsible for designating and leasing areas of the outer continental shelf for potential development in federal waters (> 3 nm offshore). The designation of areas for offshore wind energy development (i.e., WEAs) is guided by both national and state goals for renewable energy production and by marine spatial planning efforts that seek to avoid or minimize conflicts with important ecological components (e.g., critical habitat and species-of-interest) and ocean users (e.g., fishing and shipping industries). As of December 2024, there have been four WEAs proposed off the coasts of California and Oregon (Table 1). The two proposed WEAs off California are located respectively off Morro Bay and Humboldt in the north and are ~30 and 50 km offshore in water depths > 500m

Table 1. Summary of geographic properties and prevalence of seabird species from visual surveys within areas examined in the present study including the broader California Current reference areas, U.S. National Marine Sanctuaries, and offshore Wind Energy Areas (see Fig 1). BFAL = black-footed albatross; CAAU = Cassin's auklet; COMU = common murre; RHAU = rhinoceros auklet; SOSH = sooty shearwater.

Location	Type	Lat [°N]	Long [°W]	Shore Distance [km]	Depth [m]	Area [km ²]	# of segments	BFAL	CAAU	COMU	RHAU	SOSH
Study Area* Shelf**	California Current	30 - 48	117 - 127	0 - 273	0 - 4517	1.28*10 ⁶	103805	0.05	0.09	0.15	0.07	0.17
				0 - 155	0-200	57230	27404	0.03	0.11	0.44	0.13	0.27
Channel Islands†	National Marine Sanctuary	33.22 - 34.2	119.42 - 120.8	49 - 65	195 - 785	3807	3841	0	0.02	0	0.03	0.1
Chumash Heritage		33.8 - 35.2	119.9 - 121.7	0 - 94	0 - 3322	11766	7361	0.01	0.11	0.04	0.05	0.21
Monterey Bay		35.55 - 37.93	121.9 - 123.84	0 - 124	0 - 3733	15783	10879	0.14	0.11	0.35	0.14	0.37
Greater Farallones		37 - 38.6	122.85 - 124.4	0 - 55	0 - 3150	8534	4483	0.13	0.23	0.54	0.12	0.36
Cordell Bank		37.5 - 38	122.7 - 123.3	11 - 69	87 - 3400	3331	2095	0.25	0.31	0.31	0.14	0.42
Olympic Coast†		47.13 - 48.5	124.18 - 125.68	0 - 55	0 - 1104	8260	2689	0.04	0.1	0.72	0.57	0.37
Morro Bay, CA	Wind Energy Area	35.44 - 35.78	121.52 - 122.12	48 - 55	1099 - 1151	806	317	0	0.1	0	0.01	0.07
Humboldt, CA		40.74 - 41.14	124.54 - 124.81	31 - 40	500 - 1102	536	128	0.08	0.14	0.2	0.07	0.15
Brookings, OR		41.98 - 42.29	124.73 - 125.06	34 - 47	759 - 1147	541	71	0.03	0.11	0.03	0.01	0.14
Coos Bay, OR		43.72 - 43.95	124.85 - 125.11	59 - 71	1063 - 1328	248	45	0.16	0.13	0.04	0.04	0.24

* Area [km²] represents study area within 273 km of the coast covered by both aerial and ship-based surveys (see Fig 1).

** Area [km²] calculated as the area of grid cells <200m from 32-48°N from NOAA's 90m Coastal Relief bathymetry

† Not included in SDM analyses (see Methods).

<https://doi.org/10.1371/journal.pclm.0000687.t001>

(Fig 1). The two proposed WEAs off the coast of Oregon are respectively located off Brookings and Coos Bay ~35 and 60 km offshore in water depths >700m (Fig 1). There are a host of questions related to the potential impacts of this new industry on various components of the CCE, including seabirds [75]. A recent review suggests that the known impacts of offshore wind farms on seabirds have been consistently negative in other geographic areas [76]. In the CCE, collision risk at wind farms has previously been estimated as a function of seabird density and wind speeds [65]. However, displacement risk caused by climate-induced changes in suitable seabird habitat in the vicinity of WEAs remains unquantified. Given the cost and long lifespan of a typical offshore wind farm [~25 years; 77], it is important to consider potential species redistributions caused by this type of deleterious interaction in spatial planning efforts that seek to minimize potential ecological risks [27].

Seabird data

Our five focal species numerically dominate the CCE avifauna [61,63], and include two seasonal migrants: black-footed albatross (*Phoebastria nigripes*) and sooty shearwater (*Ardenna grisea*), that typically inhabit the region from late-winter through early fall (~March - October; Fig 1), as well as three species that are year-round residents: Cassin's auklet (*Ptychoramphus aleuticus*), rhinoceros auklet (*Cerorhinca monocerata*), and common murre (*Uria aalge*). The conservation statuses of these species range from Near-Threatened (black-footed albatross, Cassin's auklet, common

murre) to Least Concern (rhinoceros auklet, sooty shearwater) on the International Union for Conservation of Nature Red List. We used data from the at-sea survey compilation presented in [78], which collated sightings from many scientific programs operating between 1980–2017 with strip-transect data divided into segments that were typically 4 linear km but included some shorter segments. We excluded segments shorter than 500 m in accordance with [78]. This compilation (Fig A in [S1 Text](#)) includes both ship-based ($n = 91,011$ segments) and aerial transect surveys ($n = 41,215$ segments), and has been used previously to assess spatiotemporal variation in seabird distributions throughout the CCE (e.g., [63,78]).

Environmental data

Environmental data used to train SDMs included a suite of dynamic variables extracted at the center of transect segments (Fig B in [S1 Text](#)). Environmental fields were obtained from two data-assimilative ocean model products for the CCE (<https://oceanmodeling.ucsc.edu/>) - a historical reanalysis spanning 1980–2010 and a near-real-time product for 2011–2017. Both model products are based on the Regional Ocean Modeling System (ROMS) and span the CCE from 30 to 48 °N and from the coast to 134 °W at 0.1° (~10 km) horizontal resolution [79]. The environmental fields used included sea surface temperature (*sst*), total kinetic energy (*TKE*), wind stress curl (*wind_stress*), upper ocean (0–200 m averaged) buoyancy frequency (*bv*), and isothermal layer depth (*ild*, defined by a 0.5°C departure from *sst*). The standard deviation of sea surface temperature (*sst_sd*) was calculated over a 3x3 neighborhood of pixels (0.3° x 0.3°) and included to characterize the spatial variability in SST. Together, these variables represent important oceanographic predictors of seabird habitat and/or prey distribution and abundance [80–83]. To account for seasonality in distributions, photoperiod (*daylength*) was also calculated using the day of year and mean latitude for each survey location using the ‘*geosphere*’ R package [84]. We also included an oceanographic season (*season*) variable, as seabird distributions vary across the year according to breeding phenology and in response to different upwelling-related regimes within the CCE – defined as Davidson Current (Nov. 15 - March 14), Upwelling (March 15 - Aug. 14), and Oceanic (Aug. 15 - Nov. 14) seasons (see also [61,65]). These seasons also roughly track breeding seasons, when spatial distribution patterns may be influenced by the constraints of central place from a limited number of suitable colony sites. Cassin’s auklet, common murre, and rhinoceros auklet breed during the Upwelling season; black-footed albatross breed during the combined Davidson/Upwelling seasons while sooty shearwater breed in the Southern Hemisphere, primarily in the Upwelling season [35,85–87]. We also included a region (*province*) variable to allow responses to variables to differ among biogeographic provinces [62–64,88,89]: 1) South of Point Conception (~34.45° N), 2) Central, from Point Conception to Cape Mendocino (~40.44° N), and 3) North of Cape Mendocino (Fig 1A). Bathymetric depth (*z*) and the standard deviation of depth (*z_sd*) at a resolution of 0.3° were included from the ETOPO1 1 arc-minute product [90]. The standard deviation of depth broadly represents the rugosity of the seafloor, and serves as a proxy for topographic features (e.g., the continental shelf breaks, the slopes of seamounts) that act as key foraging areas for marine predators [91]. We also present outputs from SDMs fit and projected without the fixed effects of province and season given uncertainties of assuming stationarity in species-environment responses under climate change ([S2 Text](#)).

Species distribution modeling

The goal of our modelling effort was to assess the spatiotemporal distribution of suitable habitat for each species from 1980–2100. We used presence-absence data for model fitting, and refer to our model outputs as a habitat suitability index (HSI) based on the assumption that seabird species are preferentially located in physiologically favorable habitats. For each species there were many more absences than presences (Fig A in [S1 Text](#)), which can bias SDM results [92,93]. Therefore, we selected absences for each species prior to model fitting to achieve a 1:1 ratio of presences to absences [94]. An equal number of absences were randomly selected from each decile of SST values for each species to minimize potential biases to a specific region or time of year due to prominent data-rich surveys that typically occur during spring and summer (e.g., California Cooperative Oceanic Fisheries Investigations [CalCOFI]). SST was selected for absence thinning because it varies spatially

and seasonally and thus would sample absences across the range of conditions seabirds experience in the CCE. In addition, we expected SST to be relatively important in the models given the importance of temperature seabird SDMs in the region and elsewhere (e.g., [55,78]), and thus we sought to have the full range of SST conditions represented in the absences.

Boosted regression trees (BRTs) were used to fit SDMs. BRTs are efficient machine-learning models chosen for their flexibility in modelling non-linear responses, robustness to collinear predictor variables, and in accordance with established workflows that have been successfully employed for seabirds elsewhere [95] and for a range of taxa in the CCE (e.g., [83,96–98]). BRTs were fit using a tree complexity of 3, which allows each tree to model interactions among up to three variables; a bag fraction of 0.6, meaning 60% of the data was randomly sampled to train each tree, introducing stochasticity and reducing overfitting; and a learning rate that ensured that at least 1,000 trees were included in the final model for each species to balance model accuracy with generalization. These parameters have been found to lead to high performance without overfitting or sacrificing ecological realism that may occur when allowing complex variable interactions at higher tree complexities [99]. All BRTs were fit to presence-absence data with binomial response types using ‘dismo’ R package [100], which automatically selects the optimal number of trees during model fitting using 10-fold cross-validation. The relative importance of each predictor is determined based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees [99]. This metric is standardized to a relative contribution (%).

Model evaluation

For each species, we undertook multiple cross-validation analyses to assess spatiotemporal uncertainty in performance within our SDMs. First, we employed 10-fold cross-validation whereby, iteratively, data were randomly divided into 75–25% training-testing splits. Next, we used a leave-one-year-out (LOYO) cross-validation, where we withheld each year iteratively as testing data. Finally, we performed a spatial cross-validation where each biogeographic province (South, Central, & North) was iteratively withheld as testing data. For each cross-validation type (random, LOYO, & spatial), we calculated the mean (± 1 SD) area under the receiver operating characteristic curve (AUC) and true skill statistic (TSS) across withheld iterations [101].

Model projections under climate change conditions

After training on the historical reanalysis product to ensure robust model calibration using high-quality, observationally-constrained data, SDMs for each species were projected using daily 10 km resolution outputs of the same variables as in model fitting for the 1980–2100 period from three dynamically downscaled earth-system models (ESM) under an Representative Concentration Pathway (RCP) 8.5 emissions scenario [60]. The three earth-system models were the Geophysical Fluid Dynamics Laboratory (GFDL) ESM2M, Institut Pierre Simon Laplace (IPSL) CM5A-MR and the Hadley Center HadGEM2-ES (HAD) from phase 5 of the coupled model intercomparison project (CMIP5). While RCP8.5 represents a severe and potentially unlikely future scenario (8.5 W/m² radiative forcing by 2100) that assumes continued growth in fossil fuel emissions ([102]; but see [103]), it allows greatest pattern recognition by maximizing signal (climate change) to noise (climate variability and model stochasticity), and is thus useful in spatial planning applications [28]. Additionally, the three ESMs represent a wide spread of CMIP5 ensemble members, and differences between ensemble members are often greater than scenario differences [104]. GFDL under RCP8.5, for example, has a relatively low warming rate that is typical of other models under the less extreme RCP4.5 (4.5 W/m² radiative forcing by 2100) scenario (see [60] for more details).

Changes in suitable habitat overlap with boundaries of interest

Daily projections of HSI were used to assess historical (1985–2015), mid-century (2035–2065) and end-of-century (2070–2100) change across ecologically-important habitats and spatial management boundaries (Table 1). We calculated climatologies for 30-year periods of HSI scores; averaging across 30-year periods is common to ensure interannual to decadal climate variability is not inadvertently interpreted as long-term change [28]. For each area of interest, we calculated

climatologies of the mean and standard deviation of HSI scores, by oceanographic season, for historical, mid-century, and end-of-century periods. We then calculated the standard deviation of HSI scores in each grid cell across the three downscaled ESMs to highlight uncertainty across the ESMs. Areas-of-interest included the NMSs and offshore WEAs on the U.S. west coast (see [Fig 1](#)) as well as two ecologically-important CCE-wide reference areas: the shelf (<200m bottom depth) and a combined shelf-outer slope area (Shelf/Slope) within 273 km of the coastline that represented the offshore extent covered by both ship-based and aerial surveys ([Fig 1](#)).

Next, we extracted time-series of species' mean daily HSI scores for each model and subarea combination to assess intra-annual changes in HSI. Climatologies for each day of the year were calculated in each period, and the species-specific 75th percentile of HSI scores from the historical period were used to assess the proportion of the year in which highly suitable or 'core' habitat (i.e., >75th percentile of climatological HSI scores from the historical period; [\[10,98\]](#)) is present. We defined areas containing highly suitable habitat in both the historical and future period(s) as potential refugia. Finally, basic additive time-series decomposition was used to identify long-term trends of HSI by removing the seasonal (within each year) and residual (random) components. The trend component highlights longer-term patterns in HSI, potentially reflecting sustained environmental changes. For each time-series, we calculated the Time of Emergence (ToE), which identifies the point at which a trend becomes distinguishable from historical variability [\[105\]](#), as the date at which the HSI's trend component falls below or above one standard deviation from the mean HSI for the historical period.

Results

Species-specific responses to environmental variables

Overall, SST, bottom depth, daylength, and province were the most important variables with contributions to each model being species-specific ([Fig 2](#)). SST was the most important variable (> 30%) for the auklet species, with both favoring temperatures less than ~15° C. While SST was less important for the other three species, they also favored cooler temperatures. Compared to the other species, SST was relatively unimportant (< 5%) in models for sooty shearwater and common murre, and partial response curves for SST were flatter ([Fig C-G](#) in [S1 Text](#)). Bottom depth was the most important variable (39.4%) for sooty shearwater and common murre (68.4%) models, with the latter strongly favoring shelf depths <~400m, with habitat suitability elevated at the shelf break and shallower. Bottom depth was also relatively important in the black-footed albatross model, with depths >200 m favored by this species. Photoperiod had greater than 5% importance for all species. As expected, black-footed albatross and sooty shearwater were associated with longer photoperiods due to their seasonal occurrence within the CCE during spring-summer ([Fig 1C-1D](#)). Ocean season was marginally important in the sooty shearwater model (7.3%) and relatively unimportant (<5%) for all other species ([Fig C-G](#) in [S1 Text](#)). All species favored habitat in the Central and North provinces ([Fig 2](#)), with province being the most important variable for black-footed albatross (23.1%). Province was also relatively important for common murre (22.7%) and rhinoceros auklet (18.3%), and less so (<10%) for sooty shearwater and Cassin's auklet. The standard deviation of depth was moderately influential for black-footed albatross (14.3%) and Cassin's auklet (7.5%), with both favoring areas with elevated seafloor rugosity (i.e., higher values; [Fig C-D](#) in [S1 Text](#)). Upper ocean buoyancy frequency was moderately important (7.4%) only for the rhinoceros auklet model, with higher values favored, which indicate a more stable water column with higher stratification ([Fig F](#) in [S1 Text](#)). Isothermal layer depth, total kinetic energy, and wind stress were relatively unimportant (< 5%) in all models. A number of interactions between variables were important ([Table B](#) in [S1 Text](#)) with the strongest relationships between depth and either province (common murre) or daylength (Cassin's auklet, sooty shearwater), indicating different physiographic associations (e.g., distance to breeding colonies, fronts, or other features) throughout the CCE and intra-annually.

Spatial extent and suitability of historical and future seabird habitat

Climatologies of ensemble mean HSI highlighted the general habitat preferences of each species in the historical period ([Fig 3](#)). Black-footed albatross HSI was low on the continental shelf, with higher HSI areas extending offshore throughout

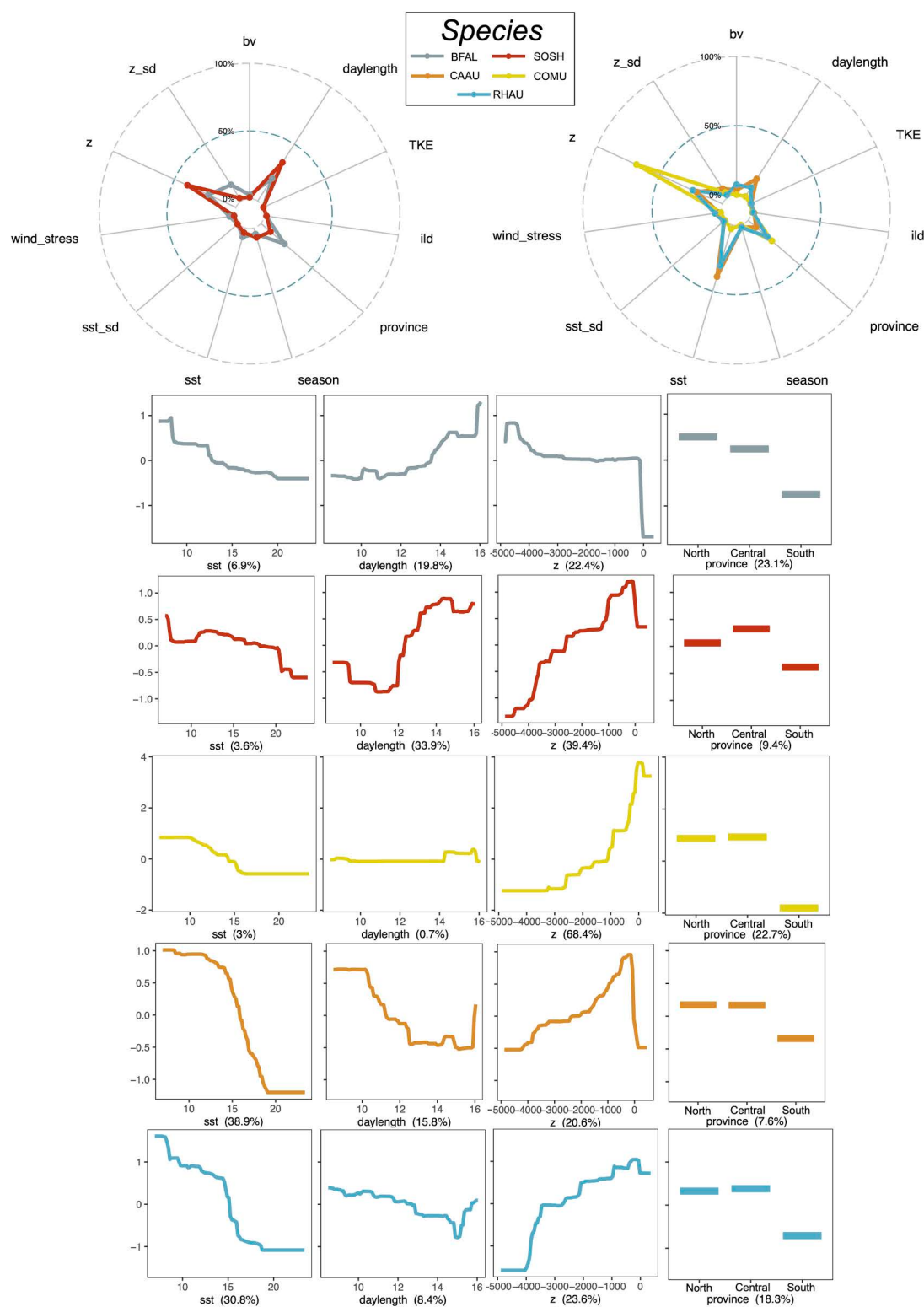


Fig 2. Variable importance in each species SDM shown in radar plots for migratory (top left) and resident species (top right). Response curves for the four most relatively important variables on average across species are shown below for each species along with their relative importance in parentheses. bv = upper ocean buoyancy frequency; TKE = total kinetic energy; ild = isothermal layer depth; sst = sea surface temperature; sst_sd = standard deviation of sea surface temperature; z = bathymetric depth; z_sd = standard deviation of depth.

<https://doi.org/10.1371/journal.pclm.0000687.g002>

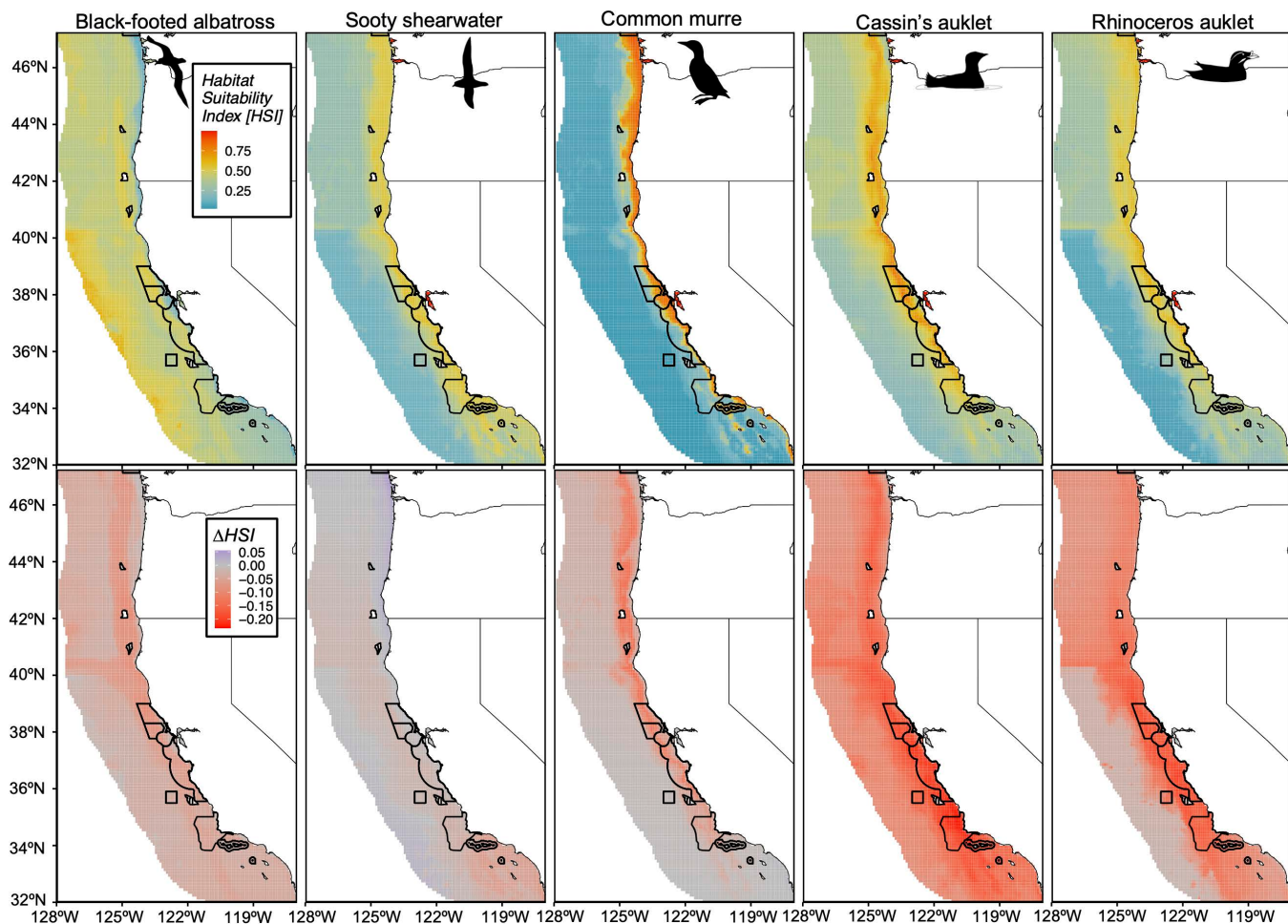


Fig 3. Mean habitat suitability index (HSI) scores in the Historical (1985-2015) period (top row) and the change in HSI (Δ HSI; bottom row) in the end-of-century (2070-2100) for each species. HSI are averaged across three downscaled earth-system models.

<https://doi.org/10.1371/journal.pclm.0000687.g003>

the extent of the shelf-outer slope study area (273 km coast-distance contour). Sooty shearwater, Cassin's auklet, and rhinoceros auklet displayed similar habitat preferences to one another, with high HSI on the shelf and upper slope and HSI gradually declining further offshore. During the historical period, HSI was generally higher for these three species within the four central CCE NMS (0.5 ± 0.07) versus for black-footed albatross and common murre (0.41 ± 0.08). This same pattern was true of the WEAs, where HSI scores for sooty shearwater and the two auklet species were higher (0.52 ± 0.07) versus for black-footed albatross and common murre (0.39 ± 0.15). Highly suitable areas (i.e., greater than the 75th percentile of historical HSI scores) were found within all four WEAs, although HSI for each species was slightly lower at the southernmost Morro Bay WEA for all species except sooty shearwater (Fig H-I in [S1 Text](#)). Both auklet species also exhibited lower HSI scores in the southern CCE, especially south of the Channel Islands. HSI scores were highest for the common murre on the continental shelf, sharply declined in areas with water depths $> \sim 400$ m and were relatively low in the southern CCE.

The strong relationship between suitability and SST in SDMs for the two auklet species led to the greatest overall HSI declines over the 21st century that extended throughout most of the study domain. These declines were slightly less pronounced in the northern CCE. Declines in HSI were also projected for black-footed albatross, common murre

and sooty shearwater resulting in relatively few areas with no change or increases in HSI that overlap with areas of high historical suitability (i.e., refugia; [Fig 3](#)). Although HSI scores for much of the coastal and continental shelf common murre habitat were stable throughout the study period, notable declines in HSI were projected in areas with depths > ~400 m. Sooty shearwater was the only species with projected increases in ensemble mean HSI, primarily along the northern CCE shelf and upper slope. Some refugia areas (i.e., little-to-no HSI changes) were also present in the northern CCE in the end-of-century and overlapped with the three WEAs in this region ([Fig 1](#) in [S1 Text](#)). The central CCE also contained end-of-century refugia for sooty shearwater, including in the four NMS ([Fig 1](#) in [S1 Text](#)).

Overall habitat across the entire year was projected to decline across the CCE for all species by 2100 ([Fig 3](#)). Time-series revealed the different rates of HSI changes and their ToEs between species, ESMs, and CCE subareas ([Fig 4](#)). Generally, emergence was later for models projected with the GFDL ESM than for HAD or IPSL, due to slower rates of physical change in GFDL, although fluctuations caused some relatively early ToEs to be detected in some of the GFDL SDM projections (e.g., most locations for CAAU). ToEs were not found for any ESM or area for sooty shearwater (i.e., long-term change never emerged from natural variability). ToEs for black-footed albatross occurred relatively later (i.e., after 2075) for black-footed albatross, and only for models projected with the HAD and IPSL ESMs, except for on the entire CCE shelf-slope, where HSI changes from GFDL emerged near the end of the century. Notably, ToEs were not found for black-footed albatross in NMSs despite an apparent declining HSI trend. Common murre ToEs for the shelf-slope study area, NMSs, and WEAs all occurred before 2050 despite a relatively lower rate of HSI decline in this species due to lower interannual variability. Relatively early (prior to 2050) ToEs were found for Cassin's auklet, which also had the greatest rate of HSI declines in the study area, although later ToEs were found in the Coos Bay WEA and the shelf-slope where emergence was not found for the GFDL projections. For rhinoceros auklet, HSI changes emerged under all three ESM projections in NMSs, while emergent changes were not found consistently across the three ESMs in the Coos Bay (HAD only) and Brookings WEAs (IPSL and HAD).

Intra-annual changes in habitat suitability in future scenarios

Within oceanographic seasons there were several refugial areas with little-to-no change or even increases in HSI ([Fig 5](#)). Across the entire CCE, the strongest HSI declines occurred in the Upwelling and Oceanic seasons, while the Davidson Current season contained the widest range of changes, including habitat losses, refugia, and gains that represent potential habitat expansions. Changes in rhinoceros auklet and Cassin's auklet HSI exemplified the variability in habitat changes across ocean seasons and provinces. In the Davidson Current season, highly suitable coastal and shelf areas in the central CCE remained suitable to the end of the century, while offshore areas were projected to decrease in HSI. HSI largely increased in the northern CCE ([Fig 5](#)). Sooty shearwater and black-footed albatross HSI was also projected to increase inshore and offshore, respectively, in the Davidson Current. In the Upwelling and Oceanic seasons, however, black-footed albatross HSI largely decreased, with some areas of little-to-no changes offshore in the central CCE ([Fig 5](#)). Meanwhile, common murre displayed the least seasonal variability. Shelf areas were projected to remain suitable for common murre near the end of the century, while potential foraging habitat seaward of the shelf break was projected to decrease in HSI. HSI increases were also apparent in the coastal southern CCE in the Oceanic and Upwelling seasons, although common murre were rarely sighted south of the Channel Islands NMS in the historical period ([Table 1](#); [Fig 1](#)). We tested the effect of excluding the fixed-effect variables of season or province by fitting additional SDMs without them. Although the results from these models were largely similar (but slightly less skillful; [Table A](#) in [S2 Text](#)), the removal of these variables did lead to small increases (~5%) in the relative importance of SST for all species except sooty shearwater. Thus, projections of these models had lower HSI scores in the southern CCE, particularly in the future, and higher variability between ESMs ([Fig A-E](#) in [S2 Text](#)).

Changes in the intra-annual timing of suitable habitat occurrence in the mid-century and end-of-century periods differed between migratory and resident species ([Fig 6](#)). HSI scores were highest for sooty shearwater and black-footed albatross

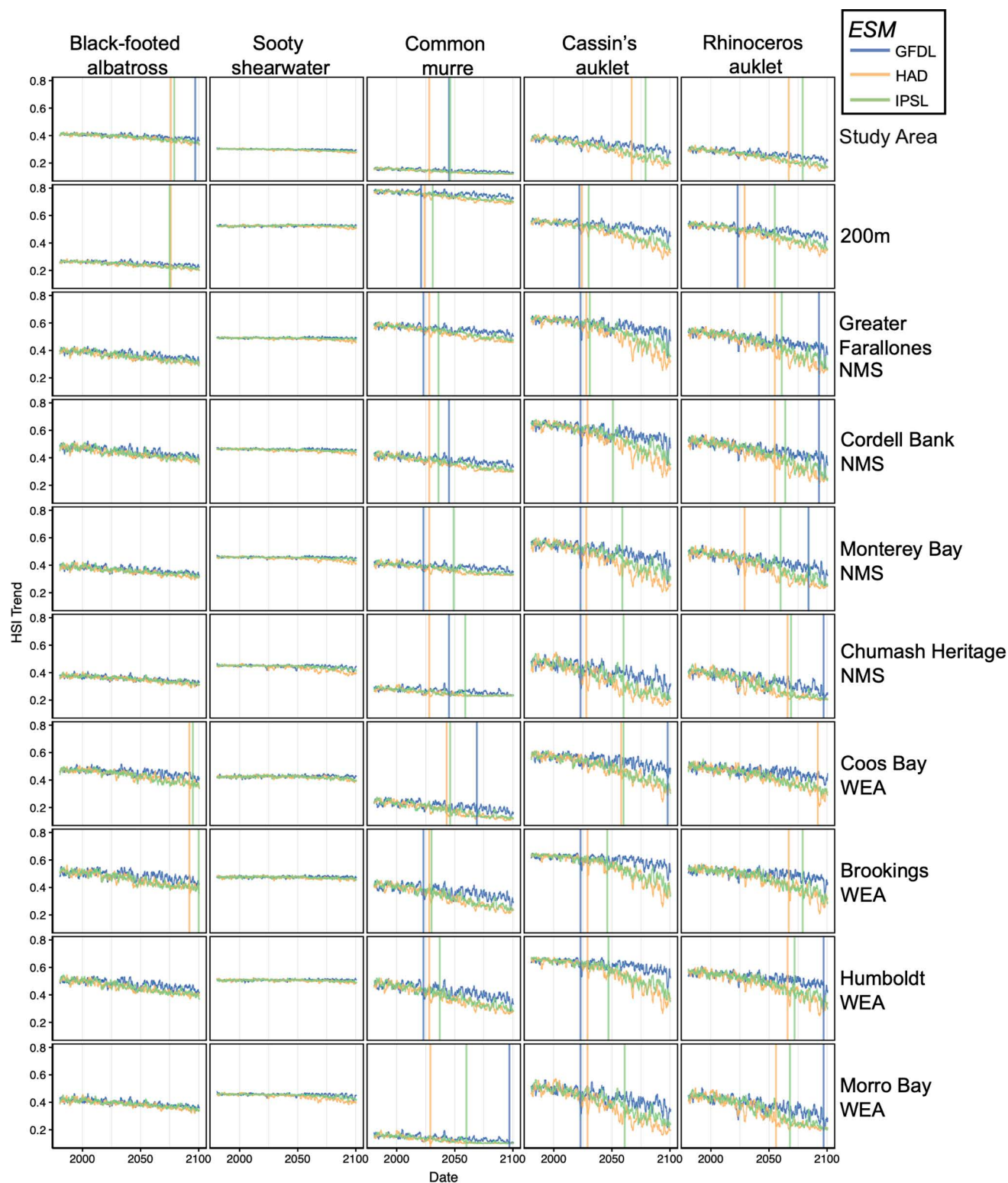


Fig 4. Habitat suitability index (HSI) trend (seasonal and random components removed) time-series and Time of Emergence (ToE; vertical lines) for changes in HSI within CCE shelf-outer slope study area (within 273 km of the coast), four National Marine Sanctuaries (NMS), and four Wind Energy Areas (WEAs) across the the Earth-System Models (colors). Both NMS & WEAs are arranged by decreasing latitude from top to bottom. ToE represents the first date where the HSI trend value is below one standard deviation of the mean HSI from the historical period (1985-2015).

<https://doi.org/10.1371/journal.pclm.0000687.g004>

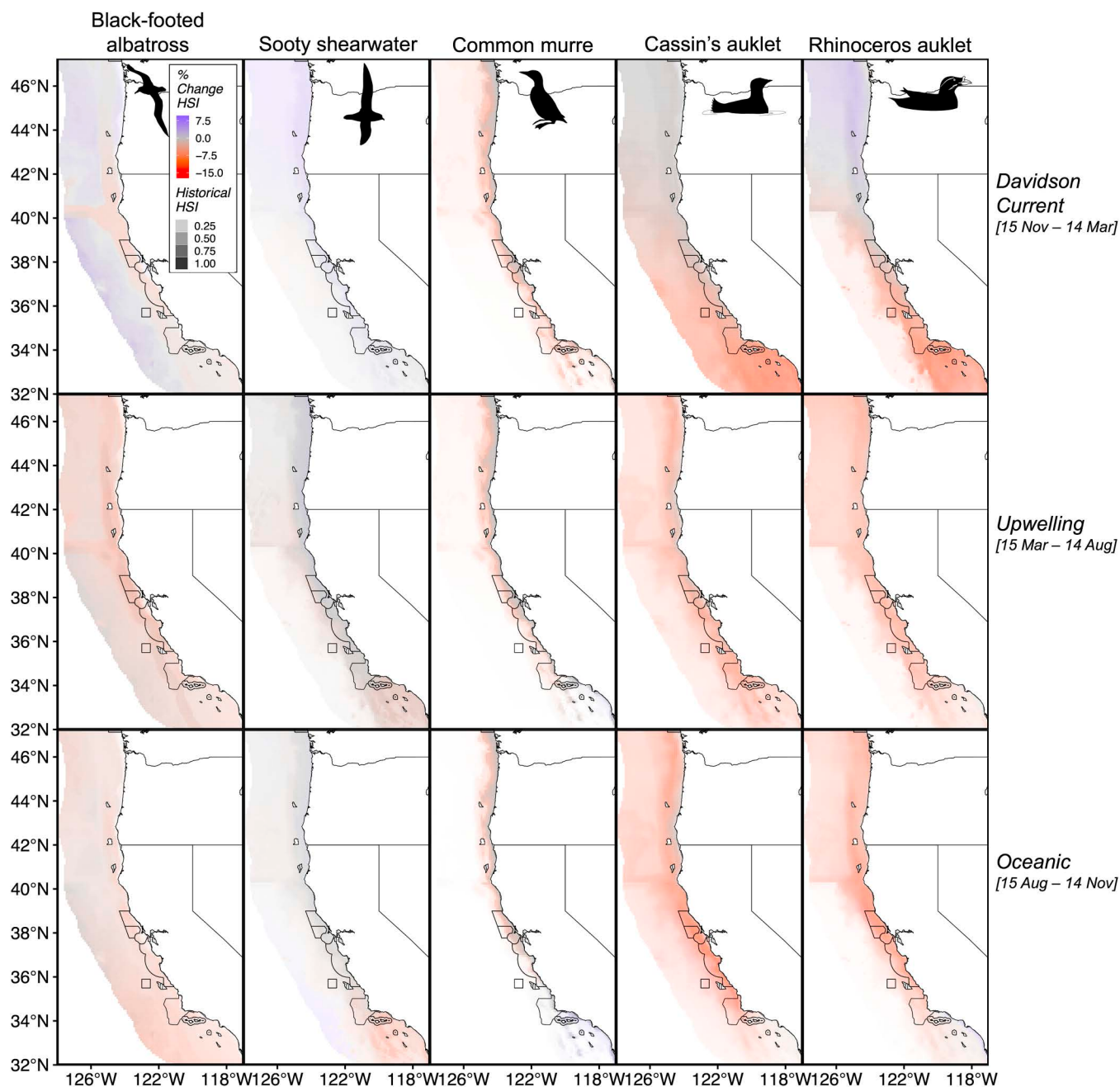


Fig 5. Mean percentage change in climatological habitat suitability index (HSI) scores [Future (2070-2100) - Historical (1985-2015)/ Historical * 100] of each species averaged across the three earth-system downscaled models for each oceanographic season. Historical HSI scores are represented by the transparency of grid cells to highlight changes in areas with relatively high historical HSI scores versus those with low historical suitability (white).

<https://doi.org/10.1371/journal.pclm.0000687.g005>

in the Upwelling season, with the latter experiencing greater declines in the number of days with highly suitable habitat (i.e., >75th percentile of historical HSI scores) in the examined areas in the mid-century and end-of-century periods (average declines of 43 and 68.14 out of 155 days, respectively). Of the areas examined, only the Humboldt, Brookings,

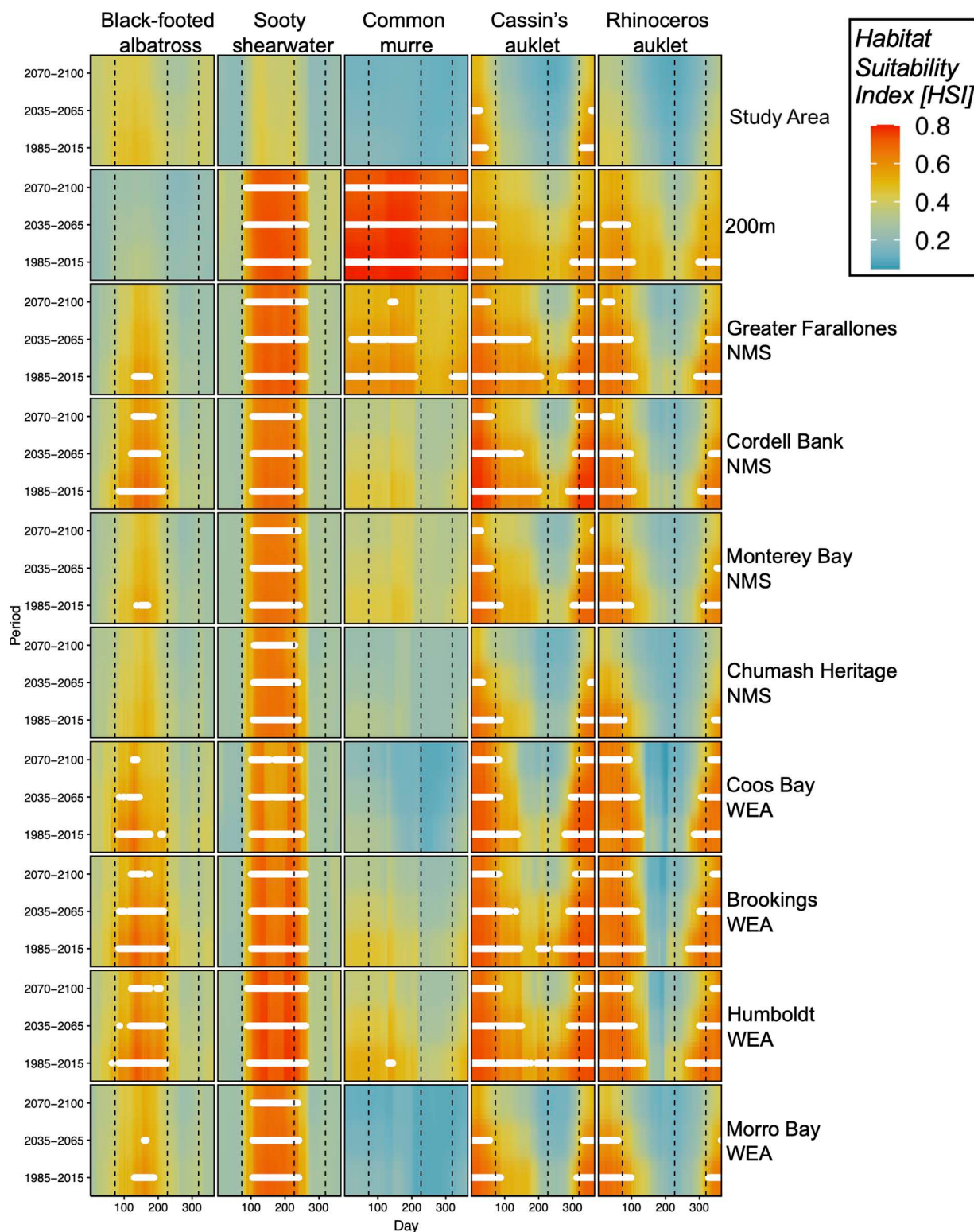


Fig 6. Daily habitat suitability index [HSI] climatologies for depicting changes in the intra-annual timing and duration of suitable habitat occurrence within the CCE in the historical (1985–2015), mid-century (2035–2065), and end-of-century (2070–2100) periods. Days with mean habitat suitability scores above the 75th percentile of each species' scores during the historical period are shown with white points. Vertical dotted lines represent CCE oceanographic seasons and are indicated in white in the top left panel; DC = Davidson Current; U = Upwelling, O = Oceanic.

<https://doi.org/10.1371/journal.pclm.0000687.g006>

and Coos Bay WEAs and the Cordell Bank NMS retained days where average conditions were highly suitable at the end-of-century for black-footed albatross (Fig 6). These declines in HSI were concentrated at the beginning and end of the Upwelling season, while HSI in the Davidson Current season was projected to remain relatively constant or even slightly increase. Common murre experienced declines in HSI throughout the year that were most pronounced in the Greater Farallones NMS and the Humboldt WEA, which respectively contained 138 and 155 days of highly suitable habitat in the historical period but had 14 and zero days at the end of century. Meanwhile, common murre HSI did not decline on the continental shelf, where average conditions were highly suitable year-round in each time period (Fig 6). Both auklet species were projected to experience HSI declines throughout the year that are concentrated in the Upwelling and Oceanic seasons, with only the Davidson Current season continuing to harbor high-HSI habitat at the end of the century for most areas except the Humboldt, Brookings, and Coos Bay WEAs, which retained some days of highly suitable habitat in the Upwelling season. The southernmost Morro Bay WEA and Chumash Heritage NMS contained highly suitable habitat for only common murre and sooty shearwater at the end of the century (Fig L-M in S1 Text).

Model uncertainty and sensitivity evaluation

Overall, performance metrics (AUC, TSS) from our cross-validation analyses revealed good-to-excellent discrimination capacity by our SDMs with AUC values ranging from 0.82 for Cassin's auklet to 0.95 for common murre (Table 2). Leave-one-year-out (LOYO) cross-validation scores were generally similar to those from random cross-validation. Meanwhile, the spatial cross-validation, in which each biogeographic province (North, Central, South; Fig 1A) was successively withheld as testing data, had slightly lower scores. Rhinoceros auklet had the most dramatic differences in performance among biogeographic provinces, with the lowest performance occurring when the North province was withheld (Fig J in S1 Text). LOYO cross-validation scores were fairly consistent across years for most species, and were lowest in years with relatively few testing data, and did not appear to notably lessen in environmentally anomalous years (e.g., 1998 El Nino; Fig J in S1 Text).

There was little divergence in projected HSI scores between the three ESMs in the historical period (Fig N in S1 Text). In the end-of-century period, the standard deviation of HSI varied by species, season, and area of the CCE (Fig O in S1 Text). Generally, uncertainty was lower in the Upwelling season, which was the most data-rich season (Table A in S1 Text). Cassin's auklet and rhinoceros auklet displayed similar patterns, with increased inter-model uncertainty north of the Greater Farallones NMS in the Oceanic season, and concentrated in the Central region in the Davidson season. Overall, inter-model differences were lower for black-footed albatross, sooty shearwater, and common murre. For common murre, uncertainty between ESMs was concentrated in the North around the shelf break and upper slope overlying the Oregon WEAs.

When the fixed effects of province and season were omitted, SDM performance slightly decreased (Table A in S2 Text). Dynamic variables such as temperature became slightly more important in the SDMs (Fig A in S2 Text), but climatologies

Table 2. Overview and evaluation of top models for each species. Mean ($\pm$ SD) skill metrics [True Skill Statistic (TSS); area under the receiver operating characteristic curve (AUC)] from SDM evaluation via random cross validation with 75-25 training-testing splits (10-fold CV), leave-one-year-out (LOYO), and spatial (by biogeographic province) cross-validation.

	10-fold CV		LOYO		Spatial	
	AUC	TSS	AUC	TSS	AUC	TSS
BFAL	0.84 $\pm$ 0.01	0.51 $\pm$ 0.02	0.78 $\pm$ 0.12	0.5 $\pm$ 0.17	0.63 $\pm$ 0.03	0.21 $\pm$ 0.05
CAAU	0.82 $\pm$ 0.01	0.5 $\pm$ 0.03	0.8 $\pm$ 0.09	0.53 $\pm$ 0.15	0.74 $\pm$ 0.05	0.38 $\pm$ 0.08
COMU	0.95 $\pm$ 0.004	0.8 $\pm$ 0.01	0.93 $\pm$ 0.06	0.79 $\pm$ 0.12	0.86 $\pm$ 0.01	0.6 $\pm$ 0.03
RHAU	0.87 $\pm$ 0.009	0.58 $\pm$ 0.02	0.86 $\pm$ 0.1	0.63 $\pm$ 0.19	0.67 $\pm$ 0.2	0.3 $\pm$ 0.27
SOSH	0.86 $\pm$ 0.006	0.59 $\pm$ 0.02	0.81 $\pm$ 0.11	0.54 $\pm$ 0.13	0.75 $\pm$ 0.06	0.42 $\pm$ 0.1

<https://doi.org/10.1371/journal.pclm.0000687.t002>

of ensemble mean HSI and standard deviation between ESMs were similar to those from models with the fixed effect variables both in the historical and end-of-century periods (Fig B-E in [S2 Text](#)). However, some differences between these two model types emerged, with models without the fixed effect variables tending to produce outputs with lower HSI in the southern CCE, and with slightly higher temporal variability (Fig F-G in [S2 Text](#)).

Discussion

Changes in atmospheric and oceanographic conditions are projected to alter the suitability of offshore and coastal habitats for many marine species. Here, we provided the first projections of how future conditions may shift the distributional patterns of five ecologically important seabird species inhabiting the CCE. The observed changes in suitable habitat suggest that our perception of the conservation benefits of marine sanctuaries or MPAs and the potential interactions between seabirds and new ocean-use development could be significantly different towards the end of the century, and that many impacts may occur by the middle of the century ([Fig 7](#)). Thus, it is important to consider the effects of future ocean conditions on species habitat suitability within marine spatial management and planning processes.

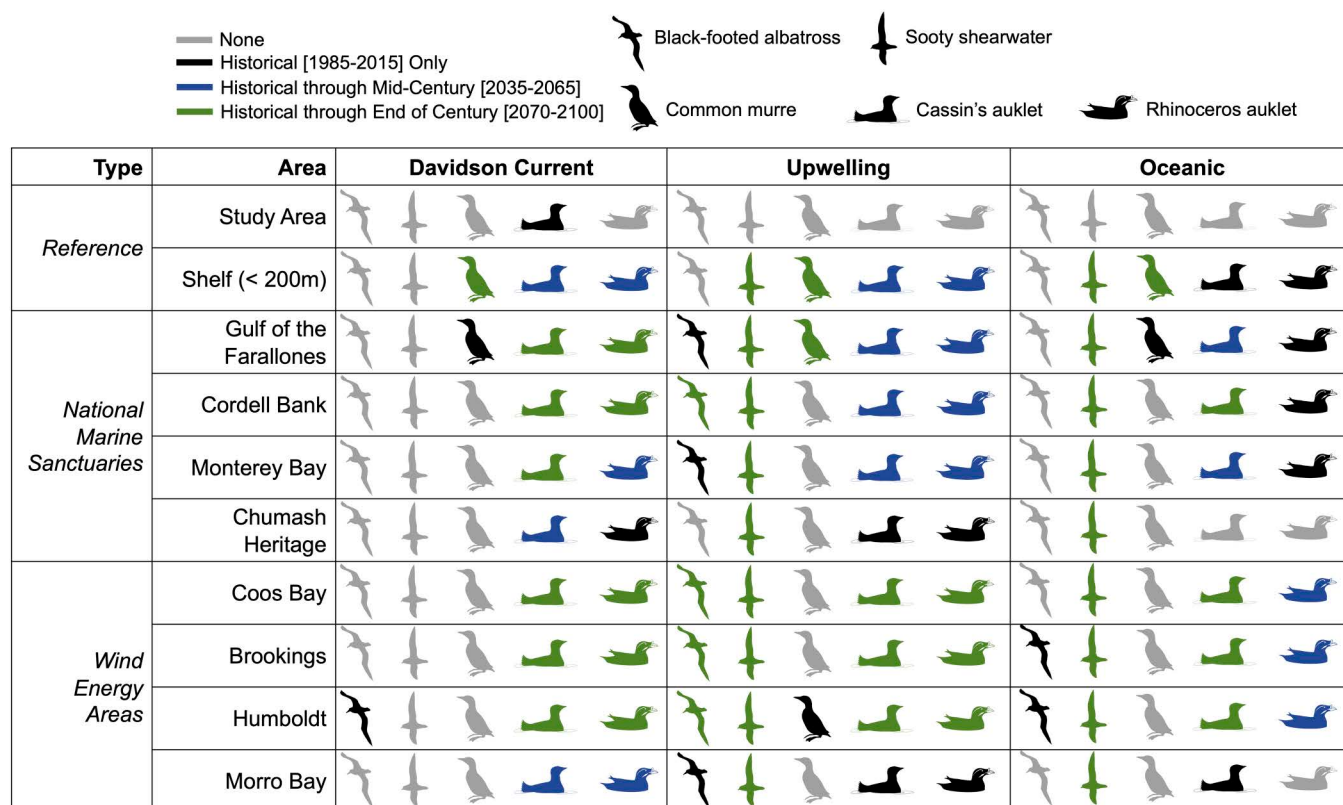


Fig 7. Summary of the distribution of highly suitable habitat (i.e., mean habitat suitability scores above the 75th percentile of each species' historical [1985-2015] scores) in each examined CCE Area (rows) and ocean season (columns) for each species (silhouettes). Silhouette colors represent whether or not (gray) the Area had mean habitat suitability scores above the 75th percentile of each species' study-wide scores during the historical (1985-2015) period on any day during each season (columns) in the historical period only (black), historical through mid-century (2035-2065; blue) or historical through the end-of-century (2070-2100; green).

<https://doi.org/10.1371/journal.pclm.0000687.g007>

Changing spatiotemporal distribution of seabird habitat

The species-specific environmental preferences we identified may provide insights into potential processes and threats that could affect seabird habitat distribution in the CCE under climate change. Important environmental variables matched previous efforts highlighting the influence of seasonality, temperature, and bathymetry as the primary physical drivers of these species' occurrence [78,106–108]. Steeper HSI declines were projected for resident alcid species than for migratory species. This was largely driven by SST, as temperature had a more moderate association with HSI for black-footed albatross, sooty shearwater and common murre. These findings are consistent with expectations of broader environmental envelopes for large-ranged, migratory species versus resident species tied to narrower ranges of local conditions [109]. Common murre, a resident species, was a notable exception whose distribution was mostly associated with bottom depth and shelf habitat north of the Southern California Bight. As the southern CCE is currently the southern range limit for the three resident species, the relatively strong declines in HSI found in the southern portion of our study area match expectations for range contractions in the CCE based on northward movement of isotherms.

However, there are many moderating factors beyond the physical environment that may contribute to changes in seabird habitat distributions under future warming scenarios. Most important is food availability, which directly drives changes in seabird population dynamics, and their habitat distribution and abundance [42,80,110]. Seabirds do not occur in isolation; foraging assemblages and biotic interactions (both mutualistic and competitive) are critical to the ecology and marine habitat use of seabirds [111,112]. Furthermore, due to elements of conservation success, the recovery of whales and pinnipeds are altering food web interactions, (e.g., [113,114]), highlighting the potential utility of joint distribution models to better understand the overlap and associations of seabirds and other taxa [115–117]. In addition, we can expect that the degree to which shifting prey resources will affect seabirds varies according to their foraging ecology (e.g., the ability to travel to offshore foraging areas), and that periods of anomalous prey availability will in turn affect the environmental preferences of species [111,118]. For example, anomalous ocean conditions caused by delayed upwelling in 2005 resulted in prey shortages (krill availability) and subsequent breeding failure of Cassin's auklets in central California, resulting in colony abandonment and distributions towards the southern CCE [119]. Migrant sooty shearwaters and black-footed albatrosses are the least geographically constrained of our focal species, and thus the relatively small HSI declines we found for these species align with their broad habitat preferences. That is, migrant species can likely shift throughout the CCE based on food availability. Meanwhile, alcids have relatively high flight costs and small foraging ranges (<100s of km) that make them sensitive to horizontal shifts in prey [120], but may be able to switch between prey to partially ameliorate the negative effects of changing availability [121–123]. For example, the magnitude of projected seabird range contractions in Great Britain and Ireland have been associated with species' foraging ecology, with smaller species that have high foraging costs and short foraging ranges the most negatively affected, as they are presumably most vulnerable to reductions in prey availability [55]. Overall, an integration of ecophysiological, behavioral, trophic, and historical factors (e.g., colony location) determine the magnitude of seabird distributional responses to changing climate and ecosystem conditions [110,124]. Therefore, the degree to which seabird habitat distributions are altered by climate change may be highly aligned with a suite of definable biological traits – particularly those related to specialization (e.g., habitat breadth) and reproductive speed (e.g., clutch size, generation time) – that may be used to quantify their climate vulnerability [125].

Timing of breeding and migration may also affect seabird species' vulnerability to spatiotemporal predator-prey mismatches, which will likely increase if phenological changes in these traits are not commensurate with changes occurring at lower trophic levels [118,126]. For example, in the Benguela Current, no-fishing areas were established around seabird breeding colonies, but the available prey within these areas shifted elsewhere in response to changes in ocean temperature and salinity, altering the previously identified conservation benefits of these static management boundaries [127]. Our projections suggest that the timing of high-quality habitat conditions for seabirds is likely to change in the future, with a general narrowing of the annual window of high-HSI conditions for all of our focal species except sooty shearwater. This equates to a temporal habitat compression that may have wide-ranging potential effects on seabirds given the seasonal

rhythms in many aspects of their ecology. For example, environmental conditions in winter that favor early upwelling has been shown to be an important indicator of breeding phenology (lay date) in common murre and Cassin's auklets in the CCE [85]. For both of these species, we found that notably large areas with neutral or positive changes in HSI in the end-of-century period occurred north of Monterey Bay during the Davidson Current season, while areas to the south declined more strongly. This suggests winter warming and associated effects on seabirds will be concentrated in the southern CCE, as is true for overall annual warming [60], and that northward shifts into more favorable biogeographic regions for certain parts of the year could be an adaptive response for these taxa. Our projected intra-annual changes in HSI also suggest that earlier arrival times might benefit migrating shearwaters and albatrosses in the future. While a general trend of earlier summer arrivals has been observed for migrating seabirds [128], it is unknown if this response will keep pace with the velocity of climate and ecosystem change.

Implications of shifts in suitable habitat for marine spatial planning and management

The ambitious goal of placing 30% of the global marine environment in protected areas [129] has gained traction in recent years [130,131], and seabirds can play an important role in the delineation and monitoring of spatial management areas as indicators of ecosystem productivity [63,110,132]. By considering future changes in habitat suitability for seabird species within NMS and WEAs, managers can include considerations for habitat protections (e.g., special wildlife zones within NMS) in management plans, reducing other stressors (e.g., actions directed at reducing interactions with fisheries or offshore wind farms), or considering potential changes to boundaries in the long-term. The four NMS of the central CCE are located in important areas for the continued study and monitoring of climate change effects on seabirds [35,63], and we found they bound areas with both high HSI in the historical scenario and notable declines in projected future HSI, particularly in the Upwelling and Oceanic seasons. This includes the areas around the Farallon Islands and Cordell Bank where a major breeding colony for resident species (Southeast Farallon Island) and key foraging grounds for migrants occur [68,106,107]. However, some areas with high historical HSI remained suitable for at least part of the year until the end of the century, and thus may become important refugia. We projected these potential seasonal refugia to occur off the coast of Oregon and Washington where NMS are mostly absent. The Olympic Coast NMS, although largely outside our model domain and thus not included in SDM analyses, has a high prevalence of our focal species and extrapolation of our results to this area would likely identify this NMS as an important refuge.

Some seasonal habitat refugia also overlapped with offshore WEA boundaries (Fig H in S1 Text), suggesting that proposed WEAs are likely to displace habitat that would have otherwise remained relatively suitable in the long term (Fig K, M in S1 Text). For example, the four WEAs contained 5 and 7.1% of highly suitable habitat grid cells that remained in the study area in the end-of-century period for sooty shearwater and Cassin's auklet, respectively. While the four proposed WEAs represent a small portion of the overall CCE seascape (1.3% of grid cells in the study area), additional research is needed to understand potential cumulative impacts. Avoidance of wind farms has been observed in many seabird species, and significant changes in abundance have been found at distances > 10 km from wind turbines [133,134], suggesting an even larger potential habitat displacement footprint than the boundaries of the WEAs used in our analyses.

While our study quantifies the availability of habitat in the vicinity of WEAs, there are additional factors that will mediate the impacts of wind farms on seabirds. [25] assessed the vulnerability across species in the CCE seabird community to collision and displacement impacts from offshore wind using a framework including population demographic and behavioral data. They found that alcids (e.g., auklets and murre) are among the most vulnerable to displacement from wind farms and relatively invulnerable to collisions, while larger-bodied, higher-flying species such as shearwaters are more vulnerable to collisions. Our analyses support the use of Cassin's auklets habitat suitability for monitoring displacement impacts of wind farms, as their historical distributions overlap with all four WEAs the most (Fig I in S1 Text) and relatively strong impacts were projected at each (Fig M in S1 Text). Common murre have shown displacement effects elsewhere [135,136], and the CCE WEAs are within the seaward limits of their foraging range and may thus displace some foraging

opportunities, particularly in the non-breeding season when foraging trips are less constrained to colony locations [137]. Similarly, the migrating, high-flying shearwaters could be used as indicators for testing the success of mitigation measures for collisions such as seasonal (or dynamic) operation scenarios (e.g., turning off or reducing the number or changing the spatial arrangement of turbines that are operating during migratory periods or when elevated wind conditions increase the likelihood of collisions [27,65]). Our SDMs could be coupled with wind models to generate short-term seasonal distribution forecasts that inform such measures. There is precedent for this type of strategy in the marine realm, such as moving fisheries closures that avoid bycatch [138], and dynamic management tools based on SDMs [139] or satellite data [140] that may show promise for meeting fishery and conservation goals.

Uncertainty, limitations, and directions for future research

Communicating uncertainty in SDMs is critical for interpreting potential climate change effects on species distributions [141]. The linkages between seabird habitat and static features such as the shelf break are well-established [78,80,106,142] and unlikely to be drastically altered in the future. However, there is considerable uncertainty in the future effect of dynamic variables, namely SST, on seabird habitat suitability. This uncertainty arises from the uncertainty inherent in ESM projections and in seabird distributions that respond to variability in ocean phenomena at multiple spatiotemporal scales [143,144] that cannot be entirely resolved by ocean models nor projected into the future. However, the declines in HSI that emerged from historical variability that we projected suggest that there may be fewer events with highly suitable conditions in the future, as habitat suitability often correlates with the upper limits of species' local abundance [145]. We examined changes in seabird habitat suitability by oceanographic season to help account for some of the uncertainty driven by seabird responses to dynamic variables. The seasonal cycle is a critical element in understanding seabird vulnerability to stressors such as offshore wind [146], and will likely remain highly relevant to seabirds given the lack of overall changes in seabird phenological traits (e.g., breeding times) observed since the mid-20th century [126]. However, there may be some alterations to seasonal patterns in the future, as projections suggest the CCE will experience intensification of upwelling in the spring and weaker summer upwelling [147] that may influence seabird phenology and the availability of prey.

Even with an extensive dataset of at-sea sightings spanning the CCE, there is also considerable uncertainty associated with the data underlying our SDMs (e.g., the distribution of survey effort). Our cross-validation exercises demonstrated the importance of assessing SDM performance and uncertainty across both spatial and temporal dimensions. The spatial cross-validation analysis suggests that biogeographic province is an important variable to include so that responses may vary between subregions within large marine ecosystems, giving SDMs additional flexibility to represent the breadth of responses across species' biogeography. Areas with relatively poor cross-validation performance (e.g., northern CCE for rhinoceros auklet) were associated with relative data scarcity, highlighting the potential use of model cross-validation outputs and other model uncertainty outputs (e.g., inter-model disagreement) to identify areas to focus monitoring and additional data collection. This also demonstrates the importance of capturing as much of species' ranges as possible when fitting SDMs, as certain areas (e.g., those with important breeding colonies) may have outsized effects on model performance.

While our projections advance our understanding of potential climate change effects on seabird habitat in the CCE, there are a number of applications and paths for future modeling efforts that may expand upon our study. For example, habitat suitability declines from seabird SDMs in other regions are spatially associated with climate-driven population declines [52], suggesting our models can provide an avenue to explore the effects of habitat quality on population variability in future studies. Abundance/density is another important dimension of seabird distributions to understand their vulnerability to climate change and the risk of interactions with offshore wind turbines. A recent study modeled the probability of aggregation occurrence [108], a quantity which may be useful to project potential changes in interactions/risk from offshore wind development [148]. SDMs based on presence-absence data should be compared with density

models, especially given uncertainties around future population changes that may affect seabird densities and the generally lower skill provided by abundance/density models, especially for taxa with patchy and high-density aggregations that may require relatively fine-scale data for realistic SDM predictions [149]. Biotic interactions (e.g., competition) between seabirds are also not included in our models, although are likely important in shaping seabird distributions given their co-occurrence and dietary overlap [111]. Joint SDMs that attempt to statistically account for species inter-dependencies may therefore be a useful tool to apply for future seabird SDMs [150].

Given the highly dynamic nature of seabird habitat use and foraging opportunities, similar projections of seabird prey habitat may also help identify additional requirements and refine projections for seabirds. Integration of forage and seabird projections would also allow for tests of whether changes in HSI between these groups are similar in magnitude or direction, and may identify associations between predator and prey habitats and refugia that would aid in future marine spatial planning efforts. Similarly, there is a growing amount of electronic tagging and behavioral data whose integration with SDMs could provide insights into foraging and migration patterns to better understand the connectivity and usage of areas we identified as highly suitable [151], or understand behavior-mediated risk of offshore wind interactions [65,136]. While tagging datasets have typically been used to evaluate SDMs or create presence-only SDMs [152,153], new methods for integrating different data types in SDMs (e.g., [154,155]) hold promise for bridging the divide between at-sea survey and tagging perspectives in seabird ecology with predictive models. Our SDMs can also be updated as new information is gathered on seabird distributions, or re-projected as ocean model products are iteratively refined or additional scenarios become available [156]. For example, the effect of large floating turbines planned for operation have been modeled in ROMS for the CCE and these models suggest that turbines will alter wind fields and oceanographic parameters in their vicinity [157,158]. These model runs may be used in future work to project these SDMs to quantify the potential ecological effects of built-out wind farms. There are many conceivable avenues for future research, the SDMs and derived outputs presented herein provide a first step in quantifying potential futures for seabird habitat across the CCE and the uncertainty associated with such projections. Our results illustrate how climate change can alter the benefits of conservation boundaries and trade-offs with proposed development, and these results could also be applied to marine spatial planning efforts for other ocean-use sectors, including offshore aquaculture, seabed mining, offshore oil and gas, wave or floating solar energy, marine carbon-dioxide removal, and commercial shipping activities.

Supporting information

S1 Text. Table A. The frequency of occurrence for each species by survey platform and oceanographic season (top) or biogeographic province (bottom). **Table B.** The relative strength of pairwise interactions between predictor variables in the SDM fit for each species. sst = sea surface temperature; z = bathymetric depth; bv = bulk buoyancy frequency; z_sd = standard deviation of depth; int.size = relative interaction size. **Fig A.** Distributions of presences by oceanographic season (colors) and absences (gray) from ship-based and aerial surveys for each species. BFAL = black-footed albatross; SOSH = sooty shearwater; COMU = common murre; CAAU = Cassin's auklet; RHAU = rhinoceros auklet. **Fig B.** Example maps showing dynamic ROMS environmental variables on April 2, 1993 from the GFDL ESM. SST = sea surface temperature; TKE = total kinetic energy; wind_stress = wind stress curl; bv = upper ocean buoyancy frequency; ild = isothermal layer depth; sst_sd = standard deviation of sea surface temperature. **Fig C.** Response curves and relative importance for all variables in the Black-footed albatross SDM. Variables are in decreasing order of relative importance (noted in parentheses). bv = upper ocean buoyancy frequency; TKE = total kinetic energy; ild = isothermal layer depth; sst = sea surface temperature; sst_sd = standard deviation of sea surface temperature; z = bathymetric depth; z_sd = standard deviation of depth. **Fig D.** Response curves and relative importance for all variables in the Cassin's auklet SDM. Variables are in decreasing order of relative importance (noted in parentheses). bv = upper ocean buoyancy frequency; TKE = total kinetic energy; ild = isothermal layer depth; sst = sea surface temperature; sst_sd = standard deviation of sea surface temperature; z = bathymetric depth; z_sd = standard deviation of depth. **Fig E.** Response

curves and relative importance for all variables in the Common murre SDM. Variables are in decreasing order of relative importance (noted in parentheses). bv = upper ocean buoyancy frequency; TKE = total kinetic energy; ild = isothermal layer depth; sst = sea surface temperature; sst_sd = standard deviation of sea surface temperature; z = bathymetric depth; z_sd = standard deviation of depth. **Fig F.** Response curves and relative importance for all variables in the Rhinoceros auklet SDM. Variables are in decreasing order of relative importance (noted in parentheses). bv = upper ocean buoyancy frequency; TKE = total kinetic energy; ild = isothermal layer depth; sst = sea surface temperature; sst_sd = standard deviation of sea surface temperature; z = bathymetric depth; z_sd = standard deviation of depth. **Fig G.** Response curves and relative importance for all variables in the Sooty shearwater SDM. Variables are in decreasing order of relative importance (noted in parentheses). bv = upper ocean buoyancy frequency; TKE = total kinetic energy; ild = isothermal layer depth; sst = sea surface temperature; sst_sd = standard deviation of sea surface temperature; z = bathymetric depth; z_sd = standard deviation of depth. **Fig H.** Changes in habitat suitability ((Future [2070–2100] - Historical [1985–2015]/ Historical * 100) $\pm$ 1 SE) within the study area (273 km coast-distance) on the CCE shelf (<200m depth), NMS, & WEAs by oceanographic season (rows). NMS & WEAs are arranged by latitude and colored by CCE biogeographic provinces. CBNMS = Cordell Bank NMS; MBNMS = Monterey Bay NMS; CHNMS = Chumash Heritage NMS. **Fig I.** Mean % of days in each year in which each examined area's mean HSI score is above the 75th percentile of scores in the historical (1985–2015) period, in each of the three study periods. CBNMS = Cordell Bank NMS; MBNMS = Monterey Bay NMS; CHNMS = Chumash Heritage NMS. **Fig J.** Temporal and spatial cross-validation results by species. Area under the receiver operating characteristic curve (AUC) and True Skill Statistic (TSS) values are shown for cross-validation folds with each year out (top two rows) or biogeographic province (bottom two rows) left out. Note that relatively few data were from 1986 and 2016–2017 (n = 56, 99 & 62, respectively; n = 575–10015 in other years) potentially leading to biased results in those years. BFAL = black-footed albatross; SOSH = sooty shearwater; COMU = common murre; CAAU = Cassin's auklet; RHAU = rhinoceros auklet. **Fig K.** The number of species in both the historical (1985–2015) and end-of-century (2070–2100) periods with highly suitable habitat (i.e., greater HSI than the 75th percentile of historical period scores) within each of the four NMS and WEAs. **Fig L.** Maps of climatological HSI in the historical period (1985–2015) and highly suitable habitat (i.e., greater HSI than the 75th percentile of historical period scores) within each of the four NMS. Points represent pixels with highly suitable habitat present in the historical period only (black) and through the end-of-century period (white). NMS are arranged by latitude (from top): Greater Farallones, Cordell Bank, Monterey Bay, and Chumash Heritage. **Fig M.** Maps of climatological HSI in the historical period (1985–2015) and highly suitable habitat (i.e., greater HSI than the 75th percentile of historical period scores) within each of the four WEAs. Points represent pixels with highly suitable habitat present in the historical period only (black) and through the end-of-century period (white). WEAs are arranged by latitude (from top): Coos Bay, Brookings, Humboldt, and Morro Bay. **Fig N.** Standard deviation of habitat suitability scores across three earth-system models for each species (columns) and oceanographic season (rows) in the historical period (1985–2015). **Fig O.** Standard deviation of habitat suitability scores across three earth-system models for each species (columns) and oceanographic season (rows) in the end-of-century period (2070–2100). (DOCX)

S2 Text. Table A. Mean ($\pm$ SD) skill metrics for models fit without fixed effect variables (province, season). True Skill Statistic (TSS) and area under the receiver operating characteristic curve (AUC) were calculated from 10-fold random cross validation with 75–25 training-testing splits. Diff_AUC = Difference in AUC between models without the fixed effect variables versus those presented in the main text. Diff_TSS = Difference in mean TSS between models without the fixed effect variables versus those presented in the main text. BFAL = black-footed albatross; SOSH = sooty shearwater; COMU = common murre; CAAU = Cassin's auklet; RHAU = rhinoceros auklet. **Fig A.** Variable importance for each species for models fit without fixed effect variables (province, season). bv = upper ocean buoyancy frequency; TKE = total kinetic energy; ild = isothermal layer depth; sst = sea surface

temperature; sst_sd = standard deviation of sea surface temperature; z = bathymetric depth; z_sd = standard deviation of depth. BFAL = black-footed albatross; SOSH = sooty shearwater; COMU = common murre; CAAU = Cassin's auklet; RHAU = rhinoceros auklet. **Fig B.** Habitat suitability index (HSI) outputs for SDMs fit with fixed effect variables (province, season) included (top row) and excluded (bottom row) in the historical (1985–2015) period. **Fig C.** Habitat suitability index (HSI) outputs for SDMs fit with fixed effect variables (province, season) included (top row) and excluded (bottom row) in the end-of-century (2070–2100) period. **Fig D.** Standard deviation of habitat suitability index (HSI SD) outputs between the three downscaled earth-system models for SDMs fit with fixed effect variables (province, season) included (top row) and excluded (bottom row) in the historical (1985–2015) period. **Fig E.** Standard deviation of habitat suitability index (HSI SD) outputs between the three downscaled earth-system models for SDMs fit with fixed effect variables (province, season) included (top row) and excluded (bottom row) in the end-of-century (2070–2100) period. **Fig F.** Differences in outputs between SDMs fit without fixed effect variables (*noFT*) and with fixed effect variables (*FT*) in the historical (1985–2015) period. Differences are shown for (a–e) ensemble mean HSI (top row) and (f–j) standard deviation of HSI between the three downscaled earth-system models. **Fig G.** Differences in outputs between SDMs fitted without fixed effect variables (*noFT*) and with fixed effect variables (*FT*) in the end-of-century (2070–2100) period. Differences are shown for (a–e) ensemble mean HSI (top row) and (f–j) standard deviation of HSI between the three downscaled earth-system models. (DOCX)

Acknowledgments

We are grateful to William Sydeman, Bill McIver, Jenny Waddell, Josh Adams, and Don Croll for assisting with seabird data for this paper. We are also grateful to all those involved in running seabird survey programs over the many decades prior to this paper, this includes but is not limited to Richard Veit, David Hyrenbach, Scott Pearson, and Craig Strong. This paper would not have been possible if not for the efforts of all those involved in coordinating and running these survey programs. We thank Rebecca Miller for providing area estimates of the continental shelf in our study area. Kelly Vasbinder provided thoughtful comments that improved the quality of this manuscript.

Author contributions

Conceptualization: Ryan Gasbarro, Kelly S. Andrews, Hannah Blondin, Megan Cimino, Thomas Clay, Elliott L. Hazen, Barbara Muhling, Nerea Lezama-Ochoa, Adena Schonfeld, Amanda Warlick, Heather Welch, Jarrod A. Santora.

Data curation: David G. Ainley, Lisa T. Ballance, Stephanie Brodie, Thomas Clay, Aspen Ellis, Joseph Evenson, Michael Jacox, Jaime Jahncke, Trevor Joyce, Jeffery B. Leirness, Nerea Lezama-Ochoa, Mercedes Pozo Buil, Amanda Warlick, Heather Welch, Jen Zamon, Kelly M. Zilliacus, Jarrod A. Santora.

Formal analysis: Ryan Gasbarro.

Funding acquisition: Kelly S. Andrews, Stephanie Brodie, Barbara Muhling, Amanda Warlick, Heather Welch, Jarrod A. Santora.

Investigation: Ryan Gasbarro, Stephanie Brodie, Jarrod A. Santora.

Methodology: Ryan Gasbarro, Stephanie Brodie.

Project administration: Ryan Gasbarro, Kelly S. Andrews, Stephanie Brodie, Megan Cimino, John C. Field, Elliott L. Hazen, Barbara Muhling, Nerea Lezama-Ochoa, Amanda Warlick, Heather Welch, Jarrod A. Santora.

Resources: Ryan Gasbarro, Kelly S. Andrews, Steven Bograd, Stephanie Brodie, Megan Cimino, Elliott L. Hazen, Jarrod A. Santora.

Software: Ryan Gasbarro, Nerea Lezama-Ochoa.

Supervision: Kelly S. Andrews, Steven Bograd, Stephanie Brodie, Megan Cimino, John C. Field, Elliott L. Hazen, Michael Jacox, Barbara Muhling, Amanda Warlick, Heather Welch, Jarrod A. Santora.

Validation: Ryan Gasbarro.

Visualization: Ryan Gasbarro.

Writing – original draft: Ryan Gasbarro, Kelly S. Andrews, Megan Cimino, Nerea Lezama-Ochoa, Jarrod A. Santora.

Writing – review & editing: Ryan Gasbarro, David G. Ainley, Kelly S. Andrews, Lisa T. Ballance, Hannah Blondin, Steven Bograd, Stephanie Brodie, Megan Cimino, Thomas Clay, Aspen Ellis, Joseph Evenson, John C. Field, Elliott L. Hazen, Michael Jacox, Jaime Jahncke, Trevor Joyce, Jeffery B. Leirness, Danielle Lipski, Barbara Muhling, Nerea Lezama-Ochoa, Mercedes Pozo Buil, Adena Schonfeld, Amanda Warlick, Heather Welch, Jen Zamon, Kelly M. Zilliacus, Jarrod A. Santora.

References

1. Calvin K, Dasgupta D, Krinner G, Mukherji A, Thorne PW, Trisos C, et al. IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland. Intergovernmental Panel on Climate Change (IPCC). 2023. <https://doi.org/10.59327/ipcc/ar6-9789291691647>
2. Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, et al. Attributing physical and biological impacts to anthropogenic climate change. *Nature*. 2008;453(7193):353–7. <https://doi.org/10.1038/nature06937> PMID: 18480817
3. Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, et al. Trophic downgrading of planet Earth. *Science*. 2011;333(6040):301–6. <https://doi.org/10.1126/science.1205106> PMID: 21764740
4. Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, English CA, et al. Climate change impacts on marine ecosystems. *Ann Rev Mar Sci*. 2012;4:11–37. <https://doi.org/10.1146/annurev-marine-041911-111611> PMID: 22457967
5. Paleczny M, Hammill E, Karpouzi V, Pauly D. Population Trend of the World's Monitored Seabirds, 1950–2010. *PLoS One*. 2015;10(6):e0129342. <https://doi.org/10.1371/journal.pone.0129342> PMID: 26058068
6. Grémillet D, Ponchon A, Paleczny M, Palomares M-LD, Karpouzi V, Pauly D. Persisting Worldwide Seabird-Fishery Competition Despite Seabird Community Decline. *Curr Biol*. 2018;28(24):4009–4013.e2. <https://doi.org/10.1016/j.cub.2018.10.051> PMID: 30528577
7. Deutsch C, Ferrel A, Seibel B, Pörtner H-O, Huey RB. Ecophysiology. Climate change tightens a metabolic constraint on marine habitats. *Science*. 2015;348(6239):1132–5. <https://doi.org/10.1126/science.aaa1605> PMID: 26045435
8. Sydeman WJ, Poloczanska E, Reed TE, Thompson SA. Climate change and marine vertebrates. *Science*. 2015;350(6262):772–7. <https://doi.org/10.1126/science.aac9874> PMID: 26564847
9. Sunday JM, Howard E, Siedlecki S, Pilcher DJ, Deutsch C, MacCready P, et al. Biological sensitivities to high-resolution climate change projections in the California current marine ecosystem. *Glob Chang Biol*. 2022;28(19):5726–40. <https://doi.org/10.1111/gcb.16317> PMID: 35899628
10. Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, et al. Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Clim Change*. 2012;3(3):234–8. <https://doi.org/10.1038/nclimate1686>
11. Wells BK, Santora JA, Henderson MJ, Warzybok P, Jahncke J, Bradley RW, et al. Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. *Journal of Marine Systems*. 2017;174:54–63. <https://doi.org/10.1016/j.jmarsys.2017.05.008>
12. Weiskopf SR, Rubenstein MA, Crozier LG, Gaichas S, Griffis R, Halofsky JE, et al. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Sci Total Environ*. 2020;733:137782. <https://doi.org/10.1016/j.scitotenv.2020.137782> PMID: 32209235
13. Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC, et al. Marine pelagic ecosystems: the west Antarctic Peninsula. *Philos Trans R Soc Lond B Biol Sci*. 2007;362(1477):67–94. <https://doi.org/10.1098/rstb.2006.1955> PMID: 17405208
14. Anderson JJ, Gurarie E, Bracis C, Burke BJ, Laidre KL. Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecological Modelling*. 2013;264:83–97. <https://doi.org/10.1016/j.ecolmodel.2013.03.009>
15. Tittensor DP, Beger M, Boerder K, Boyce DG, Cavanagh RD, Cosandey-Godin A, et al. Integrating climate adaptation and biodiversity conservation in the global ocean. *Sci Adv*. 2019;5(11):eaay9969. <https://doi.org/10.1126/sciadv.aay9969> PMID: 31807711
16. Maxwell SL, Cazalis V, Dudley N, Hoffmann M, Rodrigues ASL, Stolton S, et al. Area-based conservation in the twenty-first century. *Nature*. 2020;586(7828):217–27. <https://doi.org/10.1038/s41586-020-2773-z> PMID: 33028996
17. Jones KR, Watson JEM, Possingham HP, Klein CJ. Incorporating climate change into spatial conservation prioritisation: A review. *Biological Conservation*. 2016;194:121–30. <https://doi.org/10.1016/j.biocon.2015.12.008>
18. Bruno JF, Bates AE, Cacciapaglia C, Pike EP, Amstrup SC, van Hooedonk R, et al. Climate change threatens the world's marine protected areas. *Nature Clim Change*. 2018;8(6):499–503. <https://doi.org/10.1038/s41558-018-0149-2>

19. Pinsky ML, Rogers LA, Morley JW, Frölicher TL. Ocean planning for species on the move provides substantial benefits and requires few trade-offs. *Sci Adv*. 2020;6(50):eabb8428. <https://doi.org/10.1126/sciadv.abb8428> PMID: 33310845
20. Harvey CJ, Clay PM, Selden R, Moore SK, Andrews KS, deReynier YL, et al. Embracing social-ecological system complexity to promote climate-ready fisheries. *Rev Fish Biol Fisheries*. 2025;35(2):633–58. <https://doi.org/10.1007/s11160-025-09926-x>
21. Farr H, Ruttenberg B, Walter RK, Wang Y-H, White C. Potential environmental effects of deepwater floating offshore wind energy facilities. *Ocean & Coastal Management*. 2021;207:105611. <https://doi.org/10.1016/j.ocecoaman.2021.105611>
22. Croll DA, Ellis AA, Adams J, Cook ASCP, Garthe S, Goodale MW, et al. Framework for assessing and mitigating the impacts of offshore wind energy development on marine birds. *Biological Conservation*. 2022;276:109795. <https://doi.org/10.1016/j.biocon.2022.109795>
23. Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, et al. Threats to seabirds: A global assessment. *Biological Conservation*. 2019;237:525–37. <https://doi.org/10.1016/j.biocon.2019.06.033>
24. Garthe S, Schwemmer H, Peschko V, Markones N, Müller S, Schwemmer P, et al. Large-scale effects of offshore wind farms on seabirds of high conservation concern. *Sci Rep*. 2023;13(1):4779. <https://doi.org/10.1038/s41598-023-31601-z> PMID: 37055415
25. Kelsey EC, Felis JJ, Czapanskiy M, Pereksta DM, Adams J. Collision and displacement vulnerability to offshore wind energy infrastructure among marine birds of the Pacific Outer Continental Shelf. *J Environ Manage*. 2018;227:229–47. <https://doi.org/10.1016/j.jenvman.2018.08.051> PMID: 30195148
26. Ronconi RA, Allard KA, Taylor PD. Bird interactions with offshore oil and gas platforms: review of impacts and monitoring techniques. *J Environ Manage*. 2015;147:34–45. <https://doi.org/10.1016/j.jenvman.2014.07.031> PMID: 25261750
27. Lemos CA, Hernández M, Vilardo C, Phillips RA, Bugoni L, Sousa-Pinto I. Environmental assessment of proposed areas for offshore wind farms off southern Brazil based on ecological niche modeling and a species richness index for albatrosses and petrels. *Global Ecology and Conservation*. 2023;41:e02360. <https://doi.org/10.1016/j.gecco.2022.e02360>
28. Lezama-Ochoa N, Welch H, Brown JA, Benson SR, Forney KA, Abrahms B, et al. Identifying climate refugia and bright spots for highly mobile species. *npj Ocean Sustain*. 2025;4(1). <https://doi.org/10.1038/s44183-025-00136-3>
29. Croxall JP. *Seabirds: Feeding Ecology and Role in Marine Ecosystems*. Cambridge University Press. 1987.
30. Hamer KC, Schreiber EA, Burger J. Breeding biology, life histories, and life history–environment interactions in seabirds. In: Schreiber EA, Burger J. *Biology of Marine Birds*. Boca Raton, Florida: CRC Press. 2002. 217–61.
31. Ainley D, Ribic C, Woehler E. Adding the ocean to the study of seabirds: a brief history of at-sea seabird research. *Mar Ecol Prog Ser*. 2012;451:231–43. <https://doi.org/10.3354/meps09524>
32. Velarde E, Ezcurra E, Horn MH, Patton RT. Warm oceanographic anomalies and fishing pressure drive seabird nesting north. *Sci Adv*. 2015;1(5):e1400210. <https://doi.org/10.1126/sciadv.1400210> PMID: 26601193
33. Hazen EL, Abrahms B, Brodie S, Carroll G, Jacox MG, Savoca MS, et al. Marine top predators as climate and ecosystem sentinels. *Frontiers in Ecol & Environ*. 2019;17(10):565–74. <https://doi.org/10.1002/fee.2125>
34. Hazen EL, Savoca MS, Clark-Wolf TJ, Czapanskiy M, Rabinowitz PM, Abrahms B. Ecosystem Sentinels as Early-Warning Indicators in the Anthropocene. *Annual Review of Environment and Resources*. 2024;49(1):573–98. <https://doi.org/10.1146/annurev-environ-111522-102317>
35. Adams J, MacLeod C, Suryan RM, David Hyrenbach K, Harvey JT. Summer-time use of west coast US National Marine Sanctuaries by migrating sooty shearwaters (*Puffinus griseus*). *Biological Conservation*. 2012;156:105–16. <https://doi.org/10.1016/j.biocon.2011.12.032>
36. Felis J, Adams J, Hodum P, Carle R, Colodro V. Eastern Pacific migration strategies of pink-footed shearwaters *Ardenna creatopus*: implications for fisheries interactions and international conservation. *Endang Species Res*. 2019;39:269–82. <https://doi.org/10.3354/esr00969>
37. Oedekoven CS, Ainley DG, Spear LB. Variable responses of seabirds to change in marine climate: California Current, 1985–1994. *Marine Ecology Progress Series*. 2001;212:265–81.
38. Santora JA, Mantua NJ, Schroeder ID, Field JC, Hazen EL, Bograd SJ, et al. Habitat compression and ecosystem shifts as potential links between marine heatwave and record whale entanglements. *Nat Commun*. 2020;11(1):536. <https://doi.org/10.1038/s41467-019-14215-w> PMID: 31988285
39. Sydeman WJ, Thompson SA, Santora JA, Henry MF, Morgan KH, Batten SD. Macro-ecology of plankton-seabird associations in the North Pacific Ocean. *Journal of Plankton Research*. 2010;32(12):1697–713. <https://doi.org/10.1093/plankt/fbq119>
40. Santora JA, Ralston S, Sydeman WJ. Spatial organization of krill and seabirds in the central California Current. *ICES Journal of Marine Science*. 2011;68(7):1391–402. <https://doi.org/10.1093/icesjms/fsr046>
41. Veit R, McGowan J, Ainley D, Wahl T, Pyle P. Apex marine predator declines ninety percent in association with changing oceanic climate. *Global Change Biology*. 1997;3(1):23–8. <https://doi.org/10.1046/j.1365-2486.1997.d01-130.x>
42. Sydeman W, Mills K, Santora J, Thompson SA, Bertram D, Morgan K, et al. Seabirds and climate in the California Current—a synthesis of change. *California Cooperative Oceanic Fisheries Investigations Reports*. 2009;50.
43. Burthe S, Daunt F, Butler A, Elston D, Frederiksen M, Johns D, et al. Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Mar Ecol Prog Ser*. 2012;454:119–33. <https://doi.org/10.3354/meps09520>
44. Jones T, Parrish JK, Peterson WT, Bjorkstedt EP, Bond NA, Ballance LT, et al. Massive Mortality of a Planktivorous Seabird in Response to a Marine Heatwave. *Geophysical Research Letters*. 2018;45(7):3193–202. <https://doi.org/10.1002/2017gl076164>

45. Piatt JF, Parrish JK, Renner HM, Schoen SK, Jones TT, Arimitsu ML, et al. Extreme mortality and reproductive failure of common murrelets resulting from the northeast Pacific marine heatwave of 2014–2016. *PLoS One*. 2020;15(1):e0226087. <https://doi.org/10.1371/journal.pone.0226087> PMID: [31940310](https://pubmed.ncbi.nlm.nih.gov/31940310/)
46. Renner HM, Piatt JF, Renner M, Drummond BA, Laufenberg JS, Parrish JK. Catastrophic and persistent loss of common murrelets after a marine heatwave. *Science*. 2024;386(6727):1272–6. <https://doi.org/10.1126/science.adq4330> PMID: [39666817](https://pubmed.ncbi.nlm.nih.gov/39666817/)
47. Russell TM, Pereksta DM, Tietz JR, Vernet M, Jahncke J, Ballance LT. Increase of tropical seabirds (*Sula*) in the California Current Ecosystem with warmer ocean conditions. *Cold Spring Harbor Laboratory*. 2024. <https://doi.org/10.1101/2024.10.14.618240>
48. Bosch-Belmar M, Giommi C, Milisenda G, Abbruzzo A, Sarà G. Integrating functional traits into correlative species distribution models to investigate the vulnerability of marine human activities to climate change. *Sci Total Environ*. 2021;799:149351. <https://doi.org/10.1016/j.scitotenv.2021.149351> PMID: [34371417](https://pubmed.ncbi.nlm.nih.gov/34371417/)
49. Buenafe KCV, Dunn DC, Everett JD, Brito-Morales I, Schoeman DS, Hanson JO, et al. A metric-based framework for climate-smart conservation planning. *Ecol Appl*. 2023;33(4):e2852. <https://doi.org/10.1002/eap.2852> PMID: [36946332](https://pubmed.ncbi.nlm.nih.gov/36946332/)
50. Queirós AM, Talbot E, Beaumont NJ, Somerfield PJ, Kay S, Pascoe C, et al. Bright spots as climate-smart marine spatial planning tools for conservation and blue growth. *Glob Chang Biol*. 2021;27(21):5514–31. <https://doi.org/10.1111/gcb.15827> PMID: [34486773](https://pubmed.ncbi.nlm.nih.gov/34486773/)
51. Péron C, Weimerskirch H, Bost C-A. Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proc Biol Sci*. 2012;279(1738):2515–23. <https://doi.org/10.1098/rspb.2011.2705> PMID: [22378808](https://pubmed.ncbi.nlm.nih.gov/22378808/)
52. Russell DJF, Wanless S, Collingham YC, Anderson BJ, Beale C, Reid JB, et al. Beyond climate envelopes: bio-climate modelling accords with observed 25-year changes in seabird populations of the British Isles. *Diversity and Distributions*. 2014;21(2):211–22. <https://doi.org/10.1111/ddi.12272>
53. Legrand B, Benneveau A, Jaeger A, Pinet P, Potin G, Jaquemet S, et al. Current wintering habitat of an endemic seabird of Réunion Island, Barau's petrel *Pterodroma baraui*, and predicted changes induced by global warming. *Mar Ecol Prog Ser*. 2016;550:235–48. <https://doi.org/10.3354/meps11710>
54. Reisinger RR, Corney S, Raymond B, Lombard AT, Bester MN, Crawford RJM, et al. Habitat model forecasts suggest potential redistribution of marine predators in the southern Indian Ocean. *Diversity and Distributions*. 2021;28(1):142–59. <https://doi.org/10.1111/ddi.13447>
55. Davies J, Humphreys E, Evans T, Howells R, O'Hara-Murray R, Pearce-Higgins J. Seabird abundances projected to decline in response to climate change in Britain and Ireland. *Mar Ecol Prog Ser*. 2023;725:121–40. <https://doi.org/10.3354/meps14462>
56. Spear LB, Ainley D. The Seabird Community of the Peru Current, 1980–1995, with Comparisons to Other Eastern Boundary Currents. *MO*. 2008;36(2). <https://doi.org/10.5038/2074-1235.36.2.781>
57. Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, et al. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*. 2012;22(1):1–34. <https://doi.org/10.1017/s0959270912000020>
58. Andrews KS, Williams GD, Samhuri JF, Marshall KN, Gertseva V, Levin PS. The legacy of a crowded ocean: indicators, status, and trends of anthropogenic pressures in the California Current ecosystem. *Envir Conserv*. 2014;42(2):139–51. <https://doi.org/10.1017/s0376892914000277>
59. Miller RR, Field JC, Santora JA, Monk MH, Kosaka R, Thomson C. Spatial valuation of California marine fisheries as an ecosystem service. *Can J Fish Aquat Sci*. 2017;74(11):1732–48. <https://doi.org/10.1139/cjfas-2016-0228>
60. Pozo Buil M, Jacox MG, Fiechter J, Alexander MA, Bograd SJ, Curchitser EN, et al. A Dynamically Downscaled Ensemble of Future Projections for the California Current System. *Front Mar Sci*. 2021;8. <https://doi.org/10.3389/fmars.2021.612874>
61. Ford RG, Ainley D, Casey J, Keiper C, Spear L, Ballance L. The Biogeographic Pattern of Seabirds in the Central Portion of the California Current. *MO*. 2004;32(1). <https://doi.org/10.5038/2074-1235.32.1.601>
62. Checkley DM Jr, Barth JA. Patterns and processes in the California Current System. *Progress in Oceanography*. 2009;83(1–4):49–64. <https://doi.org/10.1016/j.pocean.2009.07.028>
63. Russell TM, Szesciorka AR, Joyce TW, Ainley DG, Ballance LT. National Marine Sanctuaries capture enhanced abundance and diversity of the California Current Ecosystem avifauna. *Journal of Marine Systems*. 2023;240:103887. <https://doi.org/10.1016/j.jmarsys.2023.103887>
64. Gasbarro R, Santora JA, Cimino M, Schonfeld A, Bograd SJ, Hazen EL, et al. Composition and Functional Diversity of Juvenile Groundfish Assemblages in the California Current. *Journal of Biogeography*. 2025;52(5). <https://doi.org/10.1111/jbi.15108>
65. Schneider SR, Wallach E, Chamberlin C, Bernstein SB, Trush S, Ainley DG, et al. Seabirds in 3D: A Framework to Evaluate Collision Vulnerability with Future Offshore Wind Developments. *Humboldt, CA: California Energy Commission*. 2024.
66. Chandler WJ, Gillelan H. The history and evolution of the National Marine Sanctuaries Act. 2004. <https://www.semanticscholar.org/paper/The-history-and-evolution-of-the-National-Marine-Chandler-Gillelan/b55279ccb9a5a87a4d95968f880f7789e99962fd>
67. Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, et al. Tracking apex marine predator movements in a dynamic ocean. *Nature*. 2011;475(7354):86–90. <https://doi.org/10.1038/nature10082> PMID: [21697831](https://pubmed.ncbi.nlm.nih.gov/21697831/)
68. Ainley DG, Lewis TJ. The History of Farallon Island Marine Bird Populations, 1854–1972. *The Condor*. 1974;76(4):432. <https://doi.org/10.2307/1365816>
69. Tarnas DA. The U.S. national marine sanctuary program: An analysis of the program's implementation and current issues. *Coastal Management*. 1988;16(4):275–303. <https://doi.org/10.1080/08920758809362064>

70. Carter HR. Oil and California's Seabirds. *MO*. 2003;31(1). <https://doi.org/10.5038/2074-1235.31.1.551>
71. Brown J, Williams GD, Harvey CJ, DeVogelaere AD, Caldwell C. Developing Science-Based Indicator Portfolios for National Marine Sanctuary Condition Reports. Silver Spring, MD: US Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries. 2019. <https://sanctuaries.noaa.gov/science/conservation/2019-science-based-indicator-portfolios.html>
72. National Oceanic and Atmospheric Administration (NOAA). Gulf of the Farallones National Marine Sanctuary final management plan. U.S. Department of Commerce. 2014. https://nmsfarallones.blob.core.windows.net/farallones-prod/media/archive/manage/pdf/expansion/GFNMS_FMP_12_04_14.pdf
73. National Oceanic and Atmospheric Administration NOAA. Cordell Bank National Marine Sanctuary final management plan. U.S. Department of Commerce. 2014. https://nmsfarallones.blob.core.windows.net/farallones-prod/media/archive/manage/pdf/expansion/CBNMS_FMP_December_2014.pdf
74. Musial W, Heimiller D, Beiter P, Scott G, Draxl C. 2016 Offshore Wind Energy Resource Assessment for the United States. Office of Scientific and Technical Information (OSTI). 2016. <https://doi.org/10.2172/1324533>
75. White C, Wang Y-H, Walter RK, Ruttenberg BI, Han D, Newman E, et al. Spatial planning offshore wind energy farms in California for mediating fisheries and wildlife conservation impacts. *Environmental Development*. 2024;51:101005. <https://doi.org/10.1016/j.envdev.2024.101005>
76. Galparsoro I, Menchaca I, Garmendia JM, Borja Á, Maldonado AD, Iglesias G, et al. Reviewing the ecological impacts of offshore wind farms. *npj Ocean Sustain*. 2022;1(1). <https://doi.org/10.1038/s44183-022-00003-5>
77. Garcia-Teruel A, Rinaldi G, Thies PR, Johanning L, Jeffrey H. Life cycle assessment of floating offshore wind farms: An evaluation of operation and maintenance. *Applied Energy*. 2022;307:118067. <https://doi.org/10.1016/j.apenergy.2021.118067>
78. Leirness JB, Adams J, Ballance LT, Coyne M, Felis JJ, Joyce T, et al. Modeling at-sea density of marine birds to support renewable energy planning on the Pacific Outer Continental Shelf of the contiguous United States. Camarillo (CA): US Department of the Interior, Bureau of Ocean Energy Management. 2021. 385.
79. Neveu E, Moore AM, Edwards CA, Fiechter J, Drake P, Crawford WJ, et al. An historical analysis of the California Current circulation using ROMS 4D-Var: System configuration and diagnostics. *Ocean Modelling*. 2016;99:133–51. <https://doi.org/10.1016/j.ocemod.2015.11.012>
80. Santora JA, Field JC, Schroeder ID, Sakuma KM, Wells BK, Sydeman WJ. Spatial ecology of krill, micronekton and top predators in the central California Current: Implications for defining ecologically important areas. *Progress in Oceanography*. 2012;106:154–74. <https://doi.org/10.1016/j.pocean.2012.08.005>
81. Santora JA, Sydeman WJ, Schroeder ID, Field JC, Miller RR, Wells BK. Persistence of trophic hotspots and relation to human impacts within an upwelling marine ecosystem. *Ecol Appl*. 2017;27(2):560–74. <https://doi.org/10.1002/eap.1466> PMID: 27862556
82. Brodie S, Jacox MG, Bograd SJ, Welch H, Dewar H, Scales KL, et al. Integrating Dynamic Subsurface Habitat Metrics Into Species Distribution Models. *Front Mar Sci*. 2018;5. <https://doi.org/10.3389/fmars.2018.00219>
83. Cimino MA, Santora JA, Schroeder I, Sydeman W, Jacox MG, Hazen EL, et al. Essential krill species habitat resolved by seasonal upwelling and ocean circulation models within the large marine ecosystem of the California Current System. *Ecography*. 2020;43(10):1536–49. <https://doi.org/10.1111/ecog.05204>
84. Hijmans RJ. geosphere: Spherical Trigonometry. 2022.
85. Schroeder I, Sydeman W, Sarkar N, Thompson S, Bograd S, Schwing F. Winter pre-conditioning of seabird phenology in the California Current. *Mar Ecol Prog Ser*. 2009;393:211–23. <https://doi.org/10.3354/meps08103>
86. Roth JE, Nur N, Warzybok P, Sydeman WJ. Annual prey consumption of a dominant seabird, the common murre, in the California Current system. *ICES Journal of Marine Science*. 2008;65(6):1046–56. <https://doi.org/10.1093/icesjms/fsn077>
87. Cross CJR, Studholme KR, Drever MC, Domalik AD, Hipfner JM, Crossin GT. Shorter Migration Distance and Breeding Latitude Correlate With Earlier Egg-Laying Across the Northeastern Pacific Ocean Range of the Rhinoceros Auklet (*Cerorhinca monocerata*). *Ecol Evol*. 2024;14(10):e70370. <https://doi.org/10.1002/ece3.70370> PMID: 39391815
88. Ainley DG. The occurrence of seabirds in the coastal region of California. *Western Birds*. 1976;7:33–68.
89. Briggs KT, Tyler WB, Lewis DB, Carlson DR. Bird communities at sea off California: 1975 to 1983. Lawrence, Kansas: Cooper Ornithological Society. 1987.
90. Amante C, Eakins BW. ETOP01 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. Technical Memorandum NESDIS NGDC-24: NOAA. 2009.
91. Ballance LT, Ainley DG, Hunt GLJ. Seabird foraging ecology. In: Steele JH, Thorpe SA, Turekian KK. *Encyclopedia of Ocean Sciences*. London: Academic Press. 2001. 2636–44.
92. Steen VA, Tingley MW, Paton PWC, Elphick CS. Spatial thinning and class balancing: Key choices lead to variation in the performance of species distribution models with citizen science data. *Methods Ecol Evol*. 2020;12(2):216–26. <https://doi.org/10.1111/2041-210x.13525>
93. Fernandez M, Sillero N, Yesson C. To be or not to be: the role of absences in niche modelling for highly mobile species in dynamic marine environments. *Ecological Modelling*. 2022;471:110040. <https://doi.org/10.1016/j.ecolmodel.2022.110040>
94. Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. Selecting pseudo-absences for species distribution models: how, where and how many?. *Methods Ecol Evol*. 2012;3(2):327–38. <https://doi.org/10.1111/j.2041-210x.2011.00172.x>

95. Opper S, Meirinho A, Ramírez I, Gardner B, O'Connell AF, Miller PI, et al. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biological Conservation*. 2012;156:94–104. <https://doi.org/10.1016/j.biocon.2011.11.013>
96. Becker EA, Forney KA, Redfern JV, Barlow J, Jacox MG, Roberts JJ, et al. Predicting cetacean abundance and distribution in a changing climate. *Diversity and Distributions*. 2018;25(4):626–43. <https://doi.org/10.1111/ddi.12867>
97. Smith JA, Pozo Buil M, Muhling B, Tommasi D, Brodie S, Frawley TH, et al. Projecting climate change impacts from physics to fisheries: A view from three California Current fisheries. *Progress in Oceanography*. 2023;211:102973. <https://doi.org/10.1016/j.pocean.2023.102973>
98. Lezama-Ochoa N, Brodie S, Welch H, Jacox MG, Pozo Buil M, Fiechter J, et al. Divergent responses of highly migratory species to climate change in the California Current. *Diversity and Distributions*. 2024;30(2):e13800. <https://doi.org/10.1111/ddi.13800>
99. Elith J, Leathwick JR, Hastie T. A working guide to boosted regression trees. *J Anim Ecol*. 2008;77(4):802–13. <https://doi.org/10.1111/j.1365-2656.2008.01390.x> PMID: 18397250
100. Hijmans RJ, Phillips S, Leathwick J, Elith J. *dismo: Species Distribution Modeling*. 2023.
101. Welch H, Savoca MS, Brodie S, Jacox MG, Muhling BA, Clay TA, et al. Impacts of marine heatwaves on top predator distributions are variable but predictable. *Nat Commun*. 2023;14(1):5188. <https://doi.org/10.1038/s41467-023-40849-y> PMID: 37669922
102. Burgess MG, Becker SL, Langendorf RE, Fredston A, Brooks CM. Climate change scenarios in fisheries and aquatic conservation research. *ICES Journal of Marine Science*. 2023;80(5):1163–78. <https://doi.org/10.1093/icesjms/fsad045>
103. Schwalm CR, Glendon S, Duffy PB. RCP8.5 tracks cumulative CO2 emissions. *Proc Natl Acad Sci U S A*. 2020;117(33):19656–7. <https://doi.org/10.1073/pnas.2007117117> PMID: 32747549
104. Goberville E, Beaugrand G, Hautekèete N-C, Piquot Y, Luczak C. Uncertainties in the projection of species distributions related to general circulation models. *Ecol Evol*. 2015;5(5):1100–16. <https://doi.org/10.1002/ece3.1411> PMID: 25798227
105. Hawkins E, Sutton R. Time of emergence of climate signals. *Geophysical Research Letters*. 2012;39(1). <https://doi.org/10.1029/2011gl005087>
106. McGowan J, Hines E, Elliott M, Howar J, Dransfield A, Nur N, et al. Using seabird habitat modeling to inform marine spatial planning in central California's National Marine Sanctuaries. *PLoS One*. 2013;8(8):e71406. <https://doi.org/10.1371/journal.pone.0071406> PMID: 23967206
107. Studwell AJ, Hines E, Elliott ML, Howar J, Holzman B, Nur N, et al. Modeling Nonresident Seabird Foraging Distributions to Inform Ocean Zoning in Central California. *PLoS One*. 2017;12(1):e0169517. <https://doi.org/10.1371/journal.pone.0169517> PMID: 28122001
108. Santora JA, Suca JJ, Cimino M, Hazen EL, Field JC, Bograd SJ, et al. Species aggregation models resolve essential foraging habitat: Implications for conservation and management. *Ecol Appl*. 2025;35(5):e70068. <https://doi.org/10.1002/eap.70068> PMID: 40605787
109. García Molinos J, Halpern BS, Schoeman DS, Brown CJ, Kiessling W, Moore PJ, et al. Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change*. 2016;6(1):Article 1. <https://doi.org/10.1038/nclimate2769>
110. Cairns DK. Seabirds as indicators of marine food supplies. *Biological Oceanography*. 1988;5:261–71.
111. Ainley D, Dugger K, Ford R, Pierce S, Reese D, Brodeur R, et al. Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. *Mar Ecol Prog Ser*. 2009;389:271–94. <https://doi.org/10.3354/meps08153>
112. Veit RR, Harrison NM. Positive Interactions among Foraging Seabirds, Marine Mammals and Fishes and Implications for Their Conservation. *Front Ecol Evol*. 2017;5. <https://doi.org/10.3389/fevo.2017.00121>
113. Ainley DG, David Hyrenbach K. Top-down and bottom-up factors affecting seabird population trends in the California current system (1985–2006). *Progress in Oceanography*. 2010;84(3–4):242–54. <https://doi.org/10.1016/j.pocean.2009.10.001>
114. Trathan PN, Ratcliffe N, Masden EA. Ecological drivers of change at South Georgia: the krill surplus, or climate variability. *Ecography*. 2012;35(11):983–93. <https://doi.org/10.1111/j.1600-0587.2012.07330.x>
115. Pollock LJ, Tingley R, Morris WK, Golding N, O'Hara RB, Parris KM, et al. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods Ecol Evol*. 2014;5(5):397–406. <https://doi.org/10.1111/2041-210x.12180>
116. Tikhonov G, Abrego N, Dunson D, Ovaskainen O. Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context. *Methods Ecol Evol*. 2017;8(4):443–52. <https://doi.org/10.1111/2041-210x.12723>
117. Kang B, Schliep EM, Gelfand AE, Clark CW, Hudak CA, Mayo CA, et al. Joint spatiotemporal modelling of zooplankton and whale abundance in a dynamic marine environment. *Journal of the Royal Statistical Society Series C: Applied Statistics*. 2025. <https://doi.org/10.1093/jrssc/qlaf038>
118. Carroll G, Abrahms B, Brodie S, Cimino MA. Spatial match-mismatch between predators and prey under climate change. *Nat Ecol Evol*. 2024;8(9):1593–601. <https://doi.org/10.1038/s41559-024-02454-0> PMID: 38914712
119. Sydeman WJ, Bradley RW, Warzybok P, Abraham CL, Jahncke J, Hyrenbach KD, et al. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking?. *Geophysical Research Letters*. 2006;33(22). <https://doi.org/10.1029/2006gl026736>
120. Adams J, Takekawa JY, Carter HR. Foraging Distance and Home Range of Cassin's Auklets Nesting at two Colonies in the California Channel Islands. *The Condor*. 2004;106(3):618–37. <https://doi.org/10.1093/condor/106.3.618>
121. Ainley D, Spear L, Allen S. Variation in the diet of Cassin's auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, USA. *Mar Ecol Prog Ser*. 1996;137:1–10. <https://doi.org/10.3354/meps137001>
122. Santora JA, Schroeder ID, Field JC, Wells BK, Sydeman WJ. Spatio-temporal dynamics of ocean conditions and forage taxa reveal regional structuring of seabird–prey relationships. *Ecol Appl*. 2014;24(7):1730–47. <https://doi.org/10.1890/13-1605.1> PMID: 29210234

123. Warzybok P, Santora JA, Ainley DG, Bradley RW, Field JC, Capitolo PJ, et al. Prey switching and consumption by seabirds in the central California Current upwelling ecosystem: Implications for forage fish management. *Journal of Marine Systems*. 2018;185:25–39. <https://doi.org/10.1016/j.jmarsys.2018.04.009>
124. Woehler E, Hobday A. Impacts of marine heatwaves may be mediated by seabird life history strategies. *Mar Ecol Prog Ser*. 2024;737:9–23. <https://doi.org/10.3354/meps14333>
125. Richards C, Cooke RSC, Bates AE. Biological traits of seabirds predict extinction risk and vulnerability to anthropogenic threats. *Global Ecol Biogeogr*. 2021;30(5):973–86. <https://doi.org/10.1111/geb.13279>
126. Keogan K, Daunt F, Wanless S, Phillips RA, Walling CA, Agnew P, et al. Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nature Clim Change*. 2018;8(4):313–8. <https://doi.org/10.1038/s41558-018-0115-z>
127. Sherley RB, Ludynia K, Dyer BM, Lamont T, Makhado AB, Roux J-P, et al. Metapopulation Tracking Juvenile Penguins Reveals an Ecosystem-wide Ecological Trap. *Curr Biol*. 2017;27(4):563–8. <https://doi.org/10.1016/j.cub.2016.12.054> PMID: 28190725
128. Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, et al. Global imprint of climate change on marine life. *Nature Clim Change*. 2013;3(10):919–25. <https://doi.org/10.1038/nclimate1958>
129. CBD. Decision adopted by the conference of the parties to the Convention on Biological Diversity 15/4 (Kunming-Montreal Global Biodiversity Framework, 2022). Convention on Biological Diversity. 2022.
130. Leadley POD, Costello MJ, Dávalos LM, Essl F, Hansen A, Hashimoto S, et al. Ecosystem area and integrity objectives of the post-2020 global biodiversity framework. Briefing note on scientific and technical issues related to the global monitoring of biodiversity. Secretariat of the Convention on Biological Diversity. 2022. 67–97.
131. Woodley S, Costello MJ, Leadley P, Mori AS, Shen X, Visconti P. Target 3: Protected and Conserved Areas. Science Briefs in Support of the Post-2020 Global Biodiversity Framework Negotiations Collated Key Messages Target 3 - Area-based Conservation Measures of Protected Areas (PAs) and Other Effective Conservation Measures (OECM). 2022. 9–18.
132. Ronconi RA, Lascelles BG, Langham GM, Reid JB, Oro D. The role of seabirds in Marine Protected Area identification, delineation, and monitoring: Introduction and synthesis. *Biological Conservation*. 2012;156:1–4. <https://doi.org/10.1016/j.biocon.2012.02.016>
133. Cook ASCP, Humphreys EM, Bennet F, Masden EA, Burton NHK. Quantifying avian avoidance of offshore wind turbines: Current evidence and key knowledge gaps. *Mar Environ Res*. 2018;140:278–88. <https://doi.org/10.1016/j.marenvres.2018.06.017> PMID: 29980294
134. Peschko V, Mendel B, Müller S, Markones N, Mercker M, Garthe S. Effects of offshore windfarms on seabird abundance: Strong effects in spring and in the breeding season. *Mar Environ Res*. 2020;162:105157. <https://doi.org/10.1016/j.marenvres.2020.105157> PMID: 33080559
135. Vanermen N, Onkelinx T, Courtens W, Van de walle M, Verstraete H, Stienen EWM. Seabird avoidance and attraction at an offshore wind farm in the Belgian part of the North Sea. *Hydrobiologia*. 2014;756(1):51–61. <https://doi.org/10.1007/s10750-014-2088-x>
136. Peschko V, Mercker M, Garthe S. Telemetry reveals strong effects of offshore wind farms on behaviour and habitat use of common guillemots (*Uria aalge*) during the breeding season. *Mar Biol*. 2020;167(8). <https://doi.org/10.1007/s00227-020-03735-5>
137. Gee S, Warzybok P, Johns ME, Jahncke J, Shaffer SA. Intra- and interannual variation in the foraging behavior of common Murres (*Uria aalge*) in the Central California current. *Journal of Experimental Marine Biology and Ecology*. 2024;575:152011. <https://doi.org/10.1016/j.jembe.2024.152011>
138. Pons M, Watson JT, Ovando D, Andraka S, Brodie S, Domingo A, et al. Trade-offs between bycatch and target catches in static versus dynamic fishery closures. *Proc Natl Acad Sci U S A*. 2022;119(4):e2114508119. <https://doi.org/10.1073/pnas.2114508119> PMID: 35058364
139. Hazen EL, Palacios DM, Forney KA, Howell EA, Becker E, Hoover AL, et al. WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. *Journal of Applied Ecology*. 2016;54(5):1415–28. <https://doi.org/10.1111/1365-2664.12820>
140. Hazen EL, Scales KL, Maxwell SM, Briscoe DK, Welch H, Bograd SJ, et al. A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Sci Adv*. 2018;4(5):eaar3001. <https://doi.org/10.1126/sciadv.aar3001> PMID: 29854945
141. Brodie S, Smith JA, Muhling BA, Barnett LAK, Carroll G, Fiedler P, et al. Recommendations for quantifying and reducing uncertainty in climate projections of species distributions. *Glob Chang Biol*. 2022;28(22):6586–601. <https://doi.org/10.1111/gcb.16371> PMID: 35978484
142. Nur N, Jahncke J, Herzog MP, Howar J, Hyrenbach KD, Zamon JE, et al. Where the wild things are: predicting hotspots of seabird aggregations in the California Current System. *Ecol Appl*. 2011;21(6):2241–57. <https://doi.org/10.1890/10-1460.1> PMID: 21939058
143. Hyrenbach KD, Veit RR. Ocean warming and seabird communities of the southern California Current System (1987–98): response at multiple temporal scales. *Deep Sea Research Part II: Topical Studies in Oceanography*. 2003;50(14–16):2537–65. [https://doi.org/10.1016/S0967-0645\(03\)00123-1](https://doi.org/10.1016/S0967-0645(03)00123-1)
144. Santora JA, Sydeman WJ. Persistence of hotspots and variability of seabird species richness and abundance in the southern California Current. *Ecosphere*. 2015;6(11):1–19. <https://doi.org/10.1890/es14-00434.1>
145. VanDerWal J, Shoo LP, Johnson CN, Williams SE. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *Am Nat*. 2009;174(2):282–91. <https://doi.org/10.1086/600087> PMID: 19519279
146. Busch M, Garthe S. Approaching population thresholds in presence of uncertainty: Assessing displacement of seabirds from offshore wind farms. *Environmental Impact Assessment Review*. 2016;56:31–42. <https://doi.org/10.1016/j.eiar.2015.08.007>
147. Brady RX, Alexander MA, Lovenduski NS, Rykaczewski RR. Emergent anthropogenic trends in California Current upwelling. *Geophysical Research Letters*. 2017;44(10):5044–52. <https://doi.org/10.1002/2017gl072945>

148. Christel I, Certain G, Cama A, Vieites DR, Ferrer X. Seabird aggregative patterns: a new tool for offshore wind energy risk assessment. *Mar Pollut Bull.* 2013;66(1–2):84–91. <https://doi.org/10.1016/j.marpolbul.2012.11.005> PMID: [23212000](https://pubmed.ncbi.nlm.nih.gov/23212000/)
149. Brambilla M, Bazzi G, Ilahiane L. The effectiveness of species distribution models in predicting local abundance depends on model grain size. *Ecology.* 2024;105(2):e4224. <https://doi.org/10.1002/ecy.4224> PMID: [38038251](https://pubmed.ncbi.nlm.nih.gov/38038251/)
150. Arimitsu ML, Piatt JF, Thorson JT, Kuletz KJ, Drew GS, Schoen SK, et al. Joint spatiotemporal models to predict seabird densities at sea. *Front Mar Sci.* 2023;10. <https://doi.org/10.3389/fmars.2023.1078042>
151. Burger AE, Shaffer SA. Application of tracking and data-logging technology in research and conservation of seabirds. *The Auk.* 2008;125(2):253–64. <https://doi.org/10.1525/auk.2008.1408>
152. Pinto C, Thorburn JA, Neat F, Wright PJ, Wright S, Scott BE, et al. Using individual tracking data to validate the predictions of species distribution models. *Diversity and Distributions.* 2016;22(6):682–93. <https://doi.org/10.1111/ddi.12437>
153. Fauchald P, Tarroux A, Amélineau F, Bråthen V, Descamps S, Ekker M, et al. Year-round distribution of Northeast Atlantic seabird populations: applications for population management and marine spatial planning. *Mar Ecol Prog Ser.* 2021;676:255–76. <https://doi.org/10.3354/meps13854>
154. Yamamoto T, Watanuki Y, Hazen EL, Nishizawa B, Sasaki H, Takahashi A. Statistical integration of tracking and vessel survey data to incorporate life history differences in habitat models. *Ecol Appl.* 2015;25(8):2394–406. <https://doi.org/10.1890/15-0142.1> PMID: [26910963](https://pubmed.ncbi.nlm.nih.gov/26910963/)
155. Mäkinen J, Merow C, Jetz W. Integrated species distribution models to account for sampling biases and improve range-wide occurrence predictions. *Global Ecol Biogeogr.* 2023;33(3):356–70. <https://doi.org/10.1111/geb.13792>
156. Sequeira AMM, Bouchet PJ, Yates KL, Mengersen K, Caley MJ. Transferring biodiversity models for conservation: Opportunities and challenges. *Methods Ecol Evol.* 2018;9(5):1250–64. <https://doi.org/10.1111/2041-210x.12998>
157. Raghukumar K, Chartrand C, Chang G, Cheung L, Roberts J. Effect of Floating Offshore Wind Turbines on Atmospheric Circulation in California. *Front Energy Res.* 2022;10. <https://doi.org/10.3389/fenrg.2022.863995>
158. Raghukumar K, Nelson T, Jacox M, Chartrand C, Fiechter J, Chang G, et al. Projected cross-shore changes in upwelling induced by offshore wind farm development along the California coast. *Commun Earth Environ.* 2023;4(1). <https://doi.org/10.1038/s43247-023-00780-y>