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Identifying climate refugia and bright spots for highly mobile species

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Climate-driven shifts in species distributions can undermine the effectiveness of protected areas. We present a framework to facilitate climate change adaptation planning by identifying where highly migratory species habitats will persist (climate refugia), emerge (bright spots), disappear (dark spots), or remain unsuitable based on model analysis by 2100. When applied to eight species in the California Current System, we found that, on average, 37% of habitats are expected to be climate refugia, 9% are bright spots, and 13% are dark spots within National Marine Sanctuaries by 2100. Species responses differ: leatherback turtles may find refuge near U.S. coastal waters (18%), blue whales may show increased bright spots (41%), and humpback whales may exhibit more dark spots (44%). These findings highlight the need to integrate species projections into spatial planning to enhance species conservation. Our approach can be applied globally to evaluate the effectiveness of protected areas in safeguarding biodiversity under climate change.

The combined impacts of climate variability and change on ecosystems are steadily increasing[1,2], with direct and indirect threats including major shifts in species distributions[3–5]. These redistributions will make area-based spatial management, including the implementation and adaptation of terrestrial and marine protected areas (MPAs), more challenging. If climate warming drives species range shifts beyond boundaries of protection, there is uncertainty in their long-term effectiveness in protecting species habitat, giving a false sense of security as species may have moved elselwhere[6–8]. Species are shifting more rapidly in the marine environment than in terrestrial ecosystems[4,9], emphasizing the timeliness of addressing this issue.

Climate-smart conservation planning is an approach to conservation that explicitly incorporates considerations of climate change into the spatial planning, design, and management of protected areas[10]. It has emerged as a critical framework that addresses the effects of climate change by integrating climate-related knowledge and supporting flexibility in changing conditions through climate change mitigation actions[11–13]. The climate-smart framework applies diverse climate-adaptation strategies to support the resilience of populations and ecosystems through the identification of the vulnerability of species and ecosystems to climate change[10]. One climate-smart strategy involves the identification of climate refugia, defined as areas of persistently high conservation value in a changing climate. These areas are characterized by unique attributes that influence species persistence or habitat stability[14,15]. Similarly, the identification of bright spots, or areas that will increase in conservation value in a changing climate[11], has also been incorporated into some climate-smart approaches. However, less attention has been given to how the effectiveness of current protected areas might change, including whether they still provide refuge for species under novel climate conditions.

Marine pelagic species, including highly mobile species such as sharks, marine mammals and turtles, play important ecological, economic and cultural roles and are integral to ecosystem structure and functioning[16]. Highly mobile species may use MPAs as well Other Effective Area-Based Conservation Measures seasonally for feeding, reproduction or migration[17,18]. Although the geographic ranges of some of these mobile species are often much larger than those of MPAs[17], making their management and protection challenging[19], the social, cultural and economic benefits they provide remain significant even with some drawbacks[20]. Climate change may require shifting protected area boundaries to account for large distributional shifts. The potential future distributions of some highly mobile species have been studied[21–23], but there is a critical need to investigate both existing (e.g., climate refugia) and future habitat suitability in relation to protected area design and management. Integrating emergent and persistent suitable habitats into a comprehensive framework is essential for effectively quantifying the risks of climate change for marine species in MPAs. This framework can also be applied to other systems, species and regions.

The goal of this study is to understand the role of MPAs as climate-smart areas for protecting highly mobile species. Specifically, we investigated

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the potential of MPAs to serve as climate refugia and bright spots by analyzing projected changes in species distributions through 2100. Based on the application of a similar previous concept[11], we implemented a methodology that combines ecological modeling and habitat suitability projections to identify patterns of spatial variability in future habitat conditions. Our study highlights key areas that may remain or become critical for species persistence under future climate scenarios.

This framework helps fulfill the needs of climate-smart management by providing detailed information on the anticipated future habitat conditions of species. As a case study for this approach, we focus on four National Marine Sanctuaries (NMS) in the California Current System (CCS): the Greater Farallones, Cordell Bank, Monterey Bay and Channel Islands (Fig. 1A). These sanctuaries were created to protect natural and cultural marine resources and are of significant importance due to their conservation, recreational, ecological, historical, scientific, educational, cultural, archeological, and/or esthetic value[24]. These areas are also hotspots for highly mobile species[25,26] that exhibit diverse habitat uses within the NMS network, including protected species that visit the NMS seasonally for feeding, reproduction or migration (e.g., leatherback turtles (*Dermochelys coriacea*) and humpback whales (*Megaptera novaeangliae*)), as well as species with high cultural or economic value (e.g., swordfish (*Xiphias gladius)* and mako sharks (*Isurus oxyrinchus*)). The incorporation of these NMS climate-smart areas in future mitigation and adaptation management plans will help to promote that sanctuary goals are maintained in the future as species and human uses of the ocean shift.

Results

We used habitat suitability models for eight highly mobile species in the California Current and projected them under three alternative climate models to assess changes in future habitat suitability within the west coast NMS. The eight species include blue (*Balaenoptera musculus*) and humpback whales, California sea lions (*Zalophus californianus*), swordfish, blue (*Prionace glauca*), thresher (*Alopias vulpinus*), and mako sharks and leatherback turtles. Our framework identifies changes in habitat suitability that fall into four categories: *dark spots (1)* are spatial areas whose habitat is projected to decrease in the future; *climate refugia (2)* are areas with consistently good habitat; conversely, *unsuitable habitat (3)* identifies areas with consistently poor habitat; and finally, *bright spots (4)* are areas with currently poor habitat suitability that are expected to emerge as more suitable in the future.

Projected species habitat

The three downscaled model projections identified highly suitable habitat for the historical period over the shelf for California sea lions, thresher sharks, and leatherbacks; along the shelf break and upper slope for humpback whales, blue whales, and blue sharks; and generally low suitability, except for higher suitability in offshore areas, for swordfish and mako sharks (Fig. 1). Blue sharks (0.60 ± 0.19), California sea lions (0.52 ± 0.24) and thresher sharks (0.47 ± 0.14) had some of the highest habitat suitability values across the NMS (Supplementary Figs. 1–4, Supplementary Table 3). An increase in habitat suitability for swordfish, blue whales, leatherback turtles and blue sharks was projected for the NMS (Supplementary Figs. 1–4, Supplementary Table 3). In contrast, humpback whales, California sea lions and thresher sharks were projected to experience a decrease in habitat suitability within the NMS (Supplementary Figs. 1–4, Supplementary Table 3).

Climate-smart areas by 2100

We found that, on average, 38% of the total sanctuary area for all the species were identified as climate refugia within the NMS, with the highest percentages of suitable habitat identified as refugia for blue sharks (98%), followed by blue whales (47%), thresher sharks (55%), California sea lions (39%), humpback whales (28%) and leatherback turtles (18%) (Fig. 2, Supplementary Table 4). On average, 9% of the

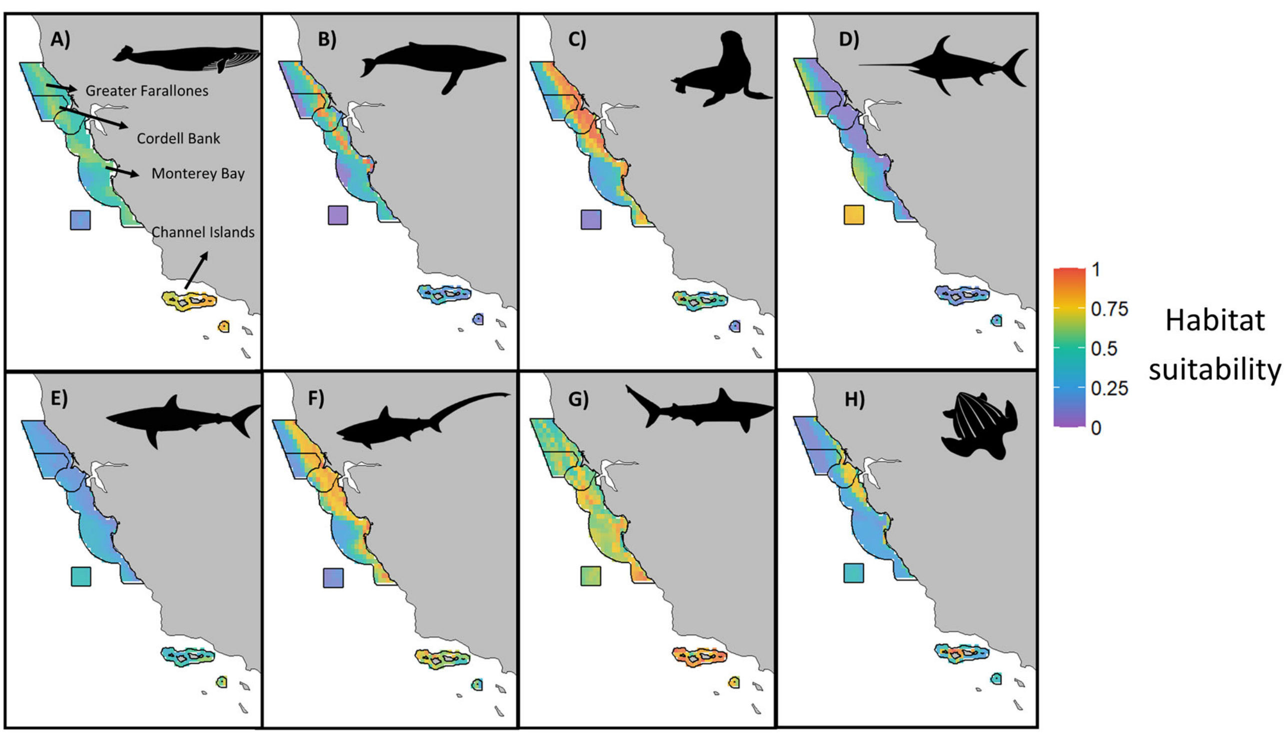

Fig. 1 | Habitat suitability averaged across three downscaled earth system models for eight highly mobile species in California's National Marine Sanctuaries (NMS), from purple = low habitat suitability (0) to red = high habitat suitability (1) for the historical period (1985–2015). The four NMS boundaries are represented by black lines and are identified in (**A**). Eight species are included (ordered by taxon): **A** blue whale, **B** humpback whale, **C** California sea lion, **D** swordfish, **E** shortfin mako shark, **F** common thresher shark, **G** blue shark, and **H** leatherback turtle. Habitat suitability maps were rescaled to 0–1 for all species to facilitate comparisons. The isolated square represents the Davidson Seamount and is part of the Monterey Bay NMS.

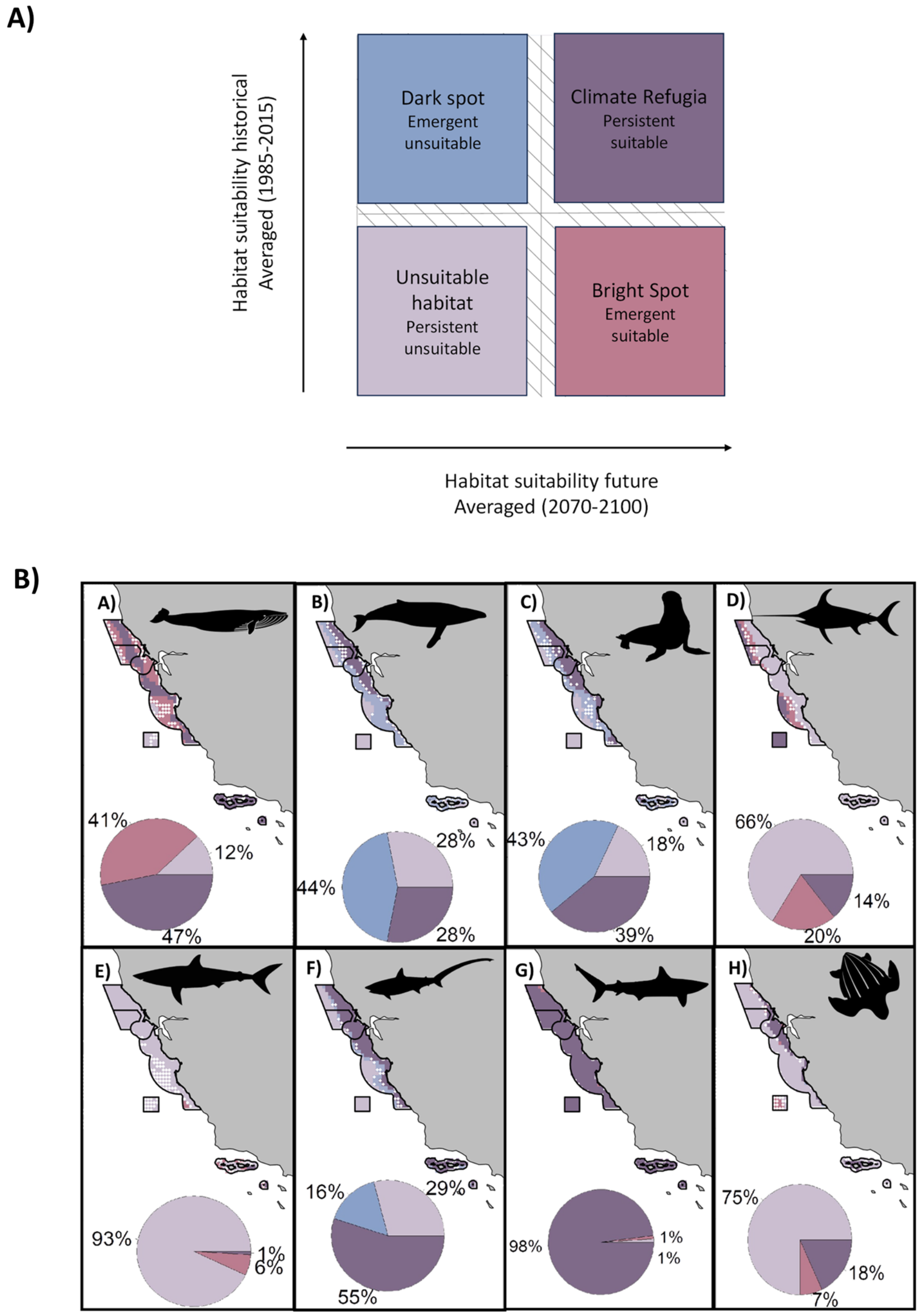

Fig. 2 | The framework used to identify four possible categories of projected change in species-specific habitat suitability for highly mobile species in California's National Marine Sanctuaries (NMS): dark spots in blue, climate refugia in purple, unsuitable habitats in lavender, and bright spots in mauve and the percentage contribution of habitat suitability for all NMSs identified with the same color scale for each species by the end of the century. The vertical axis (**A**) represents the habitat suitability (0–1) averaged across the historical period (1985–2015); the horizontal axis represents the habitat suitability (0–1) averaged across the future period (2070–2100). White crosses represent habitat suitability values (50th percentile) ±1 standard deviation to identify potential misclassification of values close to the thresholds. White dots (**B**) representing the uncertainty associated with the identification of each category are shown in Supplementary Table 5 and Supplementary Fig. 5. Pie charts for each species sum to 100%. A) blue whale, B) humpback whale, C) California sea lion, D) swordfish, E) shortfin mako shark, F) common thresher shark, G) blue shark, H) leatherback turtle. See Eq. 1 for details.

sanctuary area was identified as future bright spots, mainly for blue whales (41%) and swordfish (20%). No future dark spots were identified within the sanctuaries for 5 of the 8 species; 44%, 43% and 17% of the sanctuary area was predicted to be dark spots for the humpback whale, California sea lion and thresher shark, respectively (Supplementary Table 4). The amount of sanctuary area that remained unsuitable was highly variable across the species, ranging from a low of 1% for blue sharks to a high of 93% for shortfin mako sharks (Fig. 2, Supplementary Table 4). Classification uncertainty was low across species, with values between 1 and 3% (Supplementary Table 4). While sanctuaries contain a significant amount of bright spots for blue whales and swordfish, most of the areas predicted to be bright spots for leatherback turtles and shortfin mako people are outside of sanctuaries (Supplementary Fig. 5). Species-specific values averaged by ESM and its corresponding standard deviation are presented in (Supplementary Table 4b).

When analyzing differences according to NMS, we identified climate refugia for all species except mako shark in Greater Farallones, Cordell Bank and Monterey Bay NMS, but the percentage of habitat suitability identified as refugia varied widely among species (Fig. 3 and Supplementary Table 5). Bright spots were identified in Greater Farallones, Cordell Bank and Monterey Bay NMSs, mainly for blue whales and swordfish (a maximum of 33% for swordfish in Cordell Bank NMS and 53% for blue whales in Greater Farallones NMS) (Fig. 3). The Channel Islands NMS was identified as a bright spot for mako sharks (42%). In the case of leatherbacks, climate refugia were identified for leatherbacks in Great Farallones (26%) and Monterey NMS (15%), as were bright spots in Great Farallones (26%), Cordell Bank (6%) and Monterey (15%) NMS. Dark spots were identified in all four NMS for California sea lion, humpback whale and thresher shark (a maximum of 50% and 61% for California sea lion and humpback whales, respectively, in Channel Islands and 23% for the thresher shark in Monterey Bay).

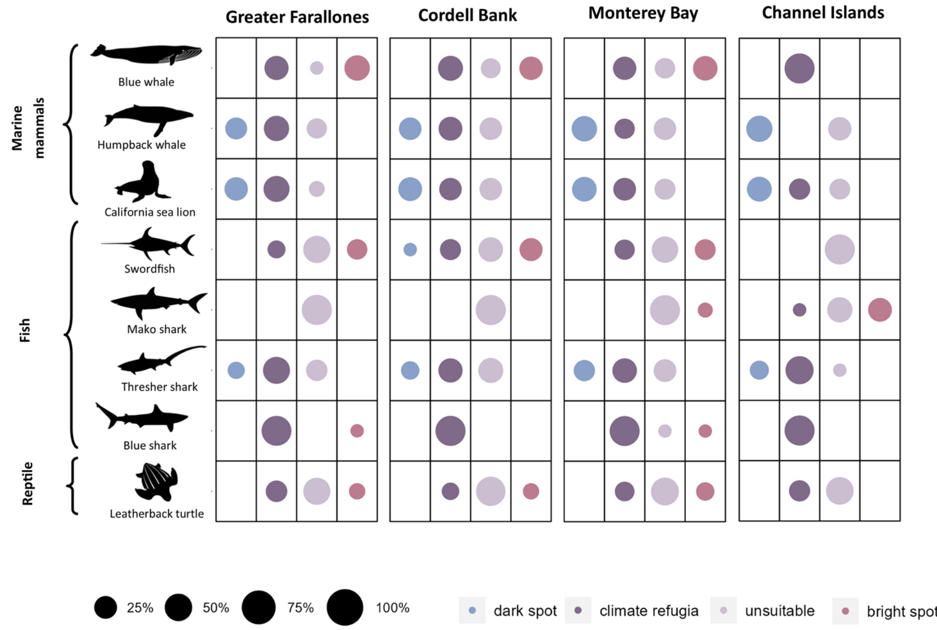

Fig. 3 | Classification of each California National Marine Sanctuary (NMS) according to the four categories of projected habitat suitability change (dark spot, climate refugia, unsuitable and bright spot) for each species. Empty grid cells represent areas not identified (e.g., 0 values). The percentage of habitat suitability identified as one of each category within each NMS was indicated by marker size. Species are ordered by taxon. The rows for each National Marine Sanctuary and species sum to 100%. See Eq. 3 for details. For species values, see Supplementary Table 5.

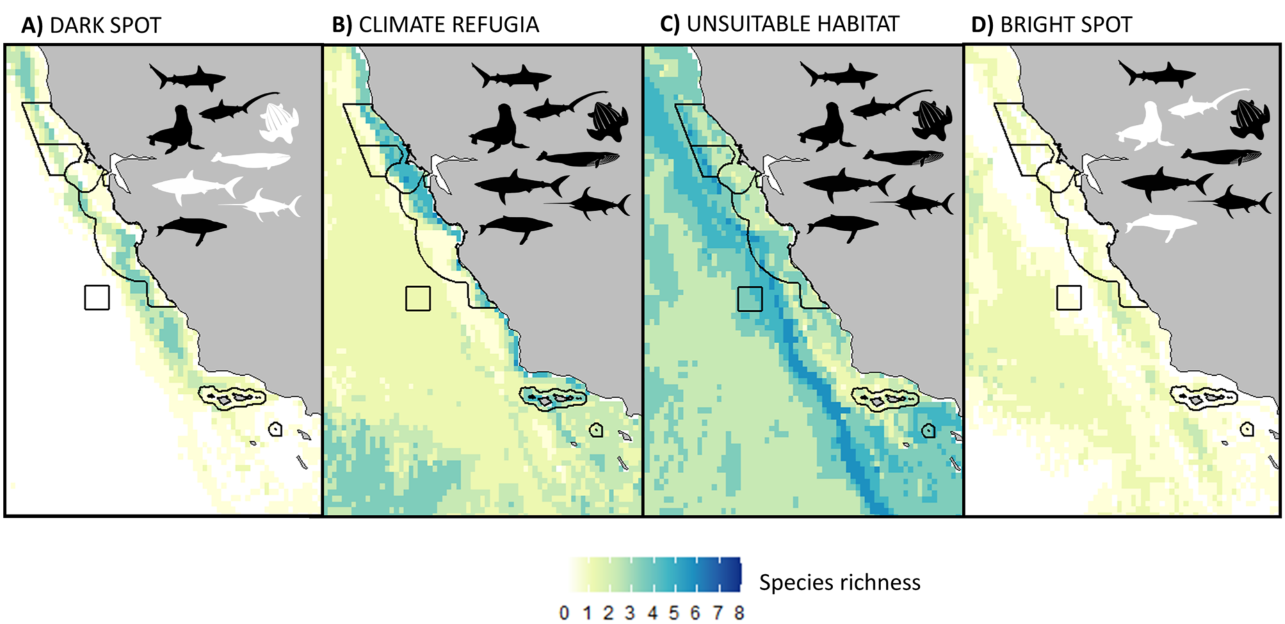

Fig. 4 | Four categories of projected habitat suitability changes (dark spot, climate refugia, unsuitable habitat, bright spot) in the CCS for eight highly mobile species. A Dark spot, **B** climate refugia, **C** unsuitable habitat and **D** bright spot. The color represents the number of species within each category (from 0 in white to 8 in dark blue). Species represented by silhouettes; white silhouettes indicate species with no location within a given climate-smart area (e.g., there are no areas classified as dark spots for swordfish).

Sanctuary areas closer to shore are predicted to serve as climate refugia for all or most of the focal species, while areas further offshore are predicted to be suitable climate refugia but for fewer species. The multispecies bright spots appear to be in the offshore areas of the Great Farallones, Cordell Bank and Monterey Sanctuaries for 2–3 species (Fig. 4). Multispecies dark spots are predicted to be found at the edge of the continental shelf and are located in the more offshore sections of the Great Farallones, Cordell Bank and Monterey NMS. Zooming out to the broader extent of the CCS enabled us to capture important areas beyond NMS. Areas within the CCS that may serve as multispecies climate refugia and bright spots were identified over the continental shelf in the northern region of California and Oregon and in areas extending offshore of the California sanctuary areas, respectively. Multi-species dark spot areas were predominantly located along the coastal regions in central and southern California. Finally, the main areas of unsuitable habitat for most or all of the focal species are anticipated to be concentrated out of NMS and in offshore regions of northern California (Fig. 4 and Supplementary Fig. 6).

Discussion

Climate-smart protected area networks require the protection of critical habitat sites and the safeguarding of climate refugia, prioritizing the species most at risk[27]. However, climate change impacts on ecosystems may be overlooked during both the design and management of protected areas[28]. Numerous studies on climate refugia that have integrated future projections have typically centered on tropical systems[29], including climate models to identify only refugia[30] or more complex climate metrics (exposure, retention) combined with climate data under different emission scenarios[10]. We developed a framework, building on an existing conceptual approach[11] to identify climate-smart areas (climate refugia, bright spots) and two additional categories (dark spot, unsuitable habitat), which we demonstrated using a case study of eight highly mobile species in California's NMS network. The results of this study can be used to support climate-smart marine spatial planning and to help managers prepare and adapt to the challenges of rapidly changing marine ecosystems. One advantage of utilizing species distribution projections organized within the framework presented here is that they can be extended to include other species, ecosystems, and regions, and the results can be integrated into the design and management of MPAs.

Targeting climate refugia and bright spots for ongoing protection under climate change can aid species in resisting and recovering from long-term perturbations while also supporting the resilience and persistence of ecosystems in the future. Each species may have potential climate refugia or bright spot areas based on its specific resistance/resilience characteristics. In this study, California's NMS were projected to contain areas of climate refugia for all eight highly mobile species (Fig. 3). Inevitably, some regions are expected to be impacted more by changes, leading to a decrease in habitat suitability for certain species (Fig. 2). There was a greater prevalence of dark spots for more coastal and resident species (e.g., humpback whales, California sea lion, and thresher shark). Species that migrate large distances to forage in coastal upwelling zones (humpback whales, blue whales, leatherbacks) are closely associated with geographical features where oceanographic conditions are projected to change (increase in temperature and decrease in chlorophyll-a[31];) and are also exposed to areas of high risk due to anthropogenic activities (fisheries, ship-strike risk, pollution, etc.) in coastal regions[32].

In addition, MPA managers could prioritize areas expected to host key species or habitats in the future or maintain suitability for a certain time period, including boundary changes, or increase protection within existing boundaries[7]. We identified these key regions withing the existing MPA boundaries as bright spots and climate refugia for species such as blue whales, swordfish, blue sharks and leatherback turtles. Increasing the protection of climate refugia and bright spots in these regions could be the most effective climate adaptation strategy available. This approach can help buffer the impacts of long-term warming on vulnerable species and provide a source of protection for nearby impacted areas[33]. For example, leatherbacks visit NMSs for critical foraging, serving as a unique hotspot along the entire west coast. If the NMS become a climate refugia area for this endangered species, it would provide a compelling reason to prioritize or enhance the area for conservation. Furthermore, areas identified as bright spots for endangered species should be considered new or expanded protected areas in future spatial planning. Even with greater protection, highly mobile species face risks of bycatch or ship strike outside of protected areas. Therefore, effective multisector management is crucial for ensuring protection across multiple life history stages.

Globally, MPAs have been increasingly impacted by climate change[6,34]. Even with protection, MPAs are decreasing in effectiveness with associated habitat and species losses throughout low-latitude and tropical areas with climate change. In contrast, as many species are expected to shift poleward, MPAs located at higher latitudes could become bright spots for species that have more compact ranges or those coming from the tropics[18]. Previous studies highlighted the importance of identifying climate refugia and bright spots as an opportunity to reduce the impacts of climate change on protected areas and improve the transition of conservation planning toward climate-smart approaches[10,11]. Our study used one of the tools (species distribution models) explored by ref. 11 to identify potential climate-smart areas and underscore the complexity of protecting species with different habitat needs.

Identifying refugia from a multispecies perspective can offer valuable insights to resource managers regarding resilient species communities[35]. The creation of networks of larger and more connected areas, such as those seen in California NMS, will be important for preventing subpopulations from being extirpated, facilitating connectivity among local populations[36–38] and providing protection as species distributions shift under climate change. Establishing connected networks would require transboundary management and collaboration with stakeholders when species move across international borders and within international waters[27,39].

As species and ecosystems respond to a changing climate, it is imperative that conservation goals are periodically re-evaluated and adapted accordingly[7]. In the U.S., NMS managers use condition reports (CRs) to evaluate the status and trends of resources and ecosystem services over the previous 10 years and use climate vulnerability assessments to identify the vulnerability of species and habitats to climate and non-climate stressors in the future to inform management priorities. The results from this study could be used to inform both of these products in California NMS and could be expanded to other NMS and MPAs[40]. Worldwide, the United Nations Convention on Biological Diversity established Aichi Target 11, aiming to protect at least 30% of the ocean by 2030 ("30 × 30") through the use of MPAs to mitigate biodiversity loss[41]. This is particularly important for highly mobile species that can benefit from local but also large and open-ocean MPAs. The largest 100 MPAs cover 7.3% of the global ocean area[41]. However, climate change assessments are still not fully incorporated into climate change management practices[42]. Monitoring programs need to identify indicators, targets and thresholds of physical change and incorporate them in MPA management adaptation plans in accordance with already established frameworks.

Our framework was useful for examining how the location and quality of suitable habitat for highly mobile species are likely to change within and around NMSs as a result of climate-driven species redistribution. This framework can be applied widely to other systems and taxa, and future research could additionally consider the integration of trophic interactions, such as future changes in predator–prey overlap[43]. Our study is based on the most extreme scenario (RCP8.5); therefore, distribution shifts may be overestimated. We recognize that our results may differ under a low-emissions scenario (e.g., RCP 3.4), if other species were included, or if species are able to adapt to some changes, such as shifts in prey availability, habitat use, or other ecological adjustments[44]. The use of additional emission scenarios based on the most realistic pathway could account for projection uncertainty alongside species distribution models and increase confidence in the identification of climate change refugia and bright spots. While we examined long-term projected changes, future studies could apply the same framework to episodic extreme events (e.g., marine heatwaves), as well as those species expected to occupy transboundary regions[26]. Short- and long-term planning could incorporate connectivity by protecting spatial corridors that allow species to track shifts between critical habitats. Pairing static management areas with dynamic MPAs, which can shift in space and time, could protect critical habitats while also tracking vulnerable populations or life histories as they shift in response to climate change[45–47].

Methods

Projected species habitat

We selected eight highly mobile species based on their economic and conservation importance from the CCS with projections published by ref. 48: the blue shark, the blue whale, the California sea lion, the common thresher shark, the humpback whale, the leatherback sea turtle, the shortfin mako shark and the swordfish (Fig. 1, see Supplementary Table 1).

Environmental variables used to build species distribution models (1980–2100) were obtained from dynamically downscaled models for the California Current. These model have a 0.1 degree resolution regional projections forced by outputs from three ~1 degree resolution Earth System Models (the Geophysical Fluid Dynamics Laboratory ESM2M, the Institute Pierre Simon Laplace CM5A-MR, and the Hadley Center HadGEM2-ES [HAD]) under a high-emission scenario: Representative Concentration Pathway (RCP) 8.5 scenario from the Coupled Model Intercomparison Project Phase 5 (CMIP5); see ref. 31 for additional details. Projections for blue shark, California sea lion, common thresher shark, humpback whale, shortfin mako shark, and swordfish were derived from daily species distribution model outputs previously fitted using boosted regression trees (BRTs) with fisheries observer data, tracking data and visual scientific survey data. Information about each species distribution model output source and projection can be found in refs. 49–52. The BRTs used presence-absence data from different sources for each species, taking a binomial distribution (Supplementary Table 1). Data for swordfish, blue shark, thresher shark and shortfin mako shark were obtained from the NOAA fisheries observer program from the California drift gillnet fishery (1990–2020). Data for California sea lion, blue shark were obtained from satellite-linked tracking data collected during the Tagging of Pacific Predators program (2001–2009)[25]. All these model outputs were projected to 2100 and published in ref. 48.

In the case of leatherback turtles, we updated the original model[52] with new available tracking data from 2011–2020. A total of 4512 presence positions (new data) for the months corresponding to January to December were collected during 2011 and 2013–2020 following the same methodology described in ref. 53. Data were cleaned to remove implausible locations collected during the tagging process (bias associated with the tagging location, the tagging devices used, track length, etc.) and to provide daily position estimates[54]. When tracks contained gaps of more than 5 days, they were split into separate bursts, defined as continuous segments of tracking data without large temporal gaps, to reduce uncertainty in position estimates and movement interpolation. The post-processing of tracking data for analysis took the following steps using the *foieGras* R package v. 0.7.6[55]: (i) removing locations associated with unrealistic swimming speeds (>10 km/h sustained over a 24-h period[56];) and (ii) fitting the data to a correlated random walk state-space model (SSM), which provided locations at a regular (daily) time interval. Once the tracks were cleaned and processed, pseudo-absence locations were randomly generated in the California Current domain (30–48°N and 115.5–134°W) by creating a set of 20 correlated random walks for each individual, which started at the tagging location and matched the total duration of the tag[57]. Presences and pseudo-absences were combined in a full dataset (Supplementary Note 1) and for each presence location, one pseudo-absence was randomly subsampled which took the same date and time stamp.

An updated leatherback model was fitted using both the old and new data following the methods used in[52]. Sea surface height (ssh) was excluded from the updated model because the dynamics controlling projected sea level changes are different from those controlling ssh variability in the historical period[48]. We validated leatherback turtle models using four different approaches: (1) full validation, (2) individual year, (3) individual latitudinal subset, and (4) individual bathymetric subset. For the full validation, the original and updated models were predicted on the full old and new tracking datasets. For the individual year, individual latitudinal subset, and individual bathymetric subset validations, the original and updated models were predicted onto each year of tracking data, and across latitudinal and bathymetric bins, for the historic and new datasets. The full validation tests overall model performance, while the latter three validations test model biases with regard to time, space, and depth. In the individual latitudinal subset validation, we used management areas defined by the International North Pacific Fisheries Commission[58] (Supplementary Note 1). We created a new latitudinal area (South = S) to include data below Conception Point. In the individual bathymetric subset validation, we divided the data into two depth bins based on the 200 m isobath. For each validation type, we calculated the area under the receiver operating characteristic curve (AUC), which measures the ability of the model to correctly predict where a species is present or absent[59]. AUC values range from 0 to 1, with 0.5 indicating that prediction is as good as random and values around 1 indicate perfect prediction. Generally, AUC values of 0.5–0.6 are considered poor, values of 0.6–0.8 are considered fair, and values of 0.8–1 are considered good. Additionally, for the full validation we calculated explained deviance, which captures how much variation in the data the model can account for. For blue whales, SDM outputs of habitat suitability were obtained from[51]. In this case, two GAMs, one for winter/spring and one for summer/fall were used for projecting habitat suitability. Both model projections were combined by weighting following[51]. GAMs were selected over BRTs because they did not include ssh and showed good performance and prediction skills. For both leatherback turtles and blue whales, habitat suitability was projected to 2100 using the same methodology described in ref. 48. For specific details, see Supplementary Note 1.

Daily habitat suitability outputs were averaged for the historic period (1985–2015) and the future period (2070–2100) for each species. These outputs were cropped to fit the boundaries of the NMS (Fig. 1). We repeat this process for each downscaled Earth system model. We calculated the mean and standard deviation of the habitat suitability values across each downscaled model to obtain the final output. It is a standard practice to average climate projections (30-year averages) so that shorter term (interannual to decadal) variability is averaged out, leaving the effect of long-term trends. To understand habitat suitability changes within MPAs from 1980–2100, we included time series for each species and NMS at an annual scale and calculated the percentage of the difference in habitat suitability between the future and the historical period.

Climate-smart areas by 2100

The framework presented here combines historical and future habitat suitability outputs for each species to identify four categories of species-specific habitat suitability projections:

- **Dark spots**—areas with high habitat suitability in the historical period but low habitat suitability in the future, interpreted as regions where suitable habitat is expected to be lost under climate change.
- **Climate refugia**—areas with high habitat suitability in both the historical and future periods, representing persistently suitable habitats that may be protected from climate impacts.
- **Unsuitable habitats**—areas with low habitat suitability in both the historical and future periods, indicating regions where unsuitable habitat is expected to persist under climate change.
- **Bright spots**—areas with low habitat suitability in the historical period but high habitat suitability in the future, interpreted as regions where emergent habitat could shift into or expand its distribution under climate change (Fig. 2).

In this study, we considered climate refugia and bright spots as climate smart areas, incorporating two additional categories. The four categories were further calculated and visualized using bivariate plots[60], which compare habitat suitability for each species across two time periods: the historical period (1985–2015) and the future period (2070–2100). To construct these bivariate plots, we followed these steps:

Calculation of the 50th percentile of habitat suitability

We used the *classIntervals* function in R (version 0.4–10[61,62]) to calculate the 50th percentile of habitat suitability for the historical period (1985–2015). Given that the range of habitat suitability values predicted for the historical period (1985–2015) may not match the future period (2070–2100), the 50th percentile of habitat suitability values from the historical period was used as a threshold to standardize the suitability ranges across both periods. This standardization enables consistent identification of categories of suitable habitats in both periods. Further details on this process are provided in Supplementary Table 2, which outlines the habitat suitability values calculated for the 50th percentile for each species and their corresponding standard deviation for the historical period (1985–2015). We also calculated the standard deviation for the historical period and applied this to the future period to account for variation in habitat suitability.

Categorization of habitat suitability

Based on the values of the 50th percentile and standard deviation, we divided the habitat suitability into the four categories: dark spots, climate refugia, unsuitable habitats, and bright spots. These categories represent different scenarios of habitat change, and each was assigned a specific value (1 or 0) in the bivariate plot. For a given species and area of interest (e.g., all sanctuaries, individual sanctuary), we calculated the fraction of pixels falling into each of the 4 categories, expressed as percentage, with the following metrics:

(A) For *all* Sanctuaries (Eq. 1): We calculated the fraction of pixels (at a resolution of 0.1°, ~10 km each), falling into each of the four categories. Additionally, we assessed the uncertainty associated with each category by calculating the percentage of pixels that fall within the 50th percentile ±standard deviation, relative to the total number of pixels in the NMS (Eq. 2).

$$A = \frac{\Sigma Xis}{\Sigma Xt} * 100 \tag{1}$$

Where A is the percentage of the sum of pixels (Σ) falling in each category *i* (dark spot, climate refugia, unsuitable habitat and bright spots) and species *s* for all the NMS (*X*) with respect to the total number of pixels *T* of all the NMS (*X*).

$$B = \Sigma Xys/\Sigma Xt * 100 \tag{2}$$

Where B is the percentage of the sum of pixels (Σ) falling in the 50th percentile ±sd for each category *y* (dark spot, climate refugia, unsuitable habitat and bright spots) and species *s* for NMS(*X*) with respect to the total number of pixels *T* of the NMS(*X*).

(B) For each individual sanctuary (Eq. 3): For each sanctuary, we repeated the same analysis, calculating the fraction of pixels falling into each of the four categories.

$$B = \Sigma Xys/\Sigma Xt * 100 \tag{3}$$

Where B is the percentage of the sum of pixels (Σ) falling in the 50th percentile ±sd for each category *y* (dark spot, climate refugia, unsuitable habitat and bright spots) and species *s* for NMS(*X*) with respect to the total number of pixels *T* of the NMS(*X*).

This can be interpreted as the extent of habitat suitability in the area of interest (A - all sanctuaries, B - individual sanctuaries) identified as dark spots, climate refugia, unsuitable habitats and bright spot areas for each species.

(C) Cumulative species presence by category or species richness (Eq. 4): To assess the collective habitat suitability changes across all species, we filtered the bivariate outputs for each species by the four categories. A value of "1" was assigned to pixels within each identified category, and a value of "0" was assigned to all other pixels. We then summed the filtered species layers for each category to assess the cumulative presence of species in each category. This allowed us to identify the overall distribution of habitat suitability changes for multiple species.

$$C = Xis/\Sigma Xt * 100 \tag{4}$$

Where C is the percentage of the number of pixels falling in each category *i* (dark spot, climate refugia, unsuitable habitat and bright spots) and species *s* for each NMS (*X*) with respect to the total number of pixels *T* of the same NMS (*X*).

Additional information about the metrics is provided in the supplementary material and discussion.

Data availability

The datasets used and/or analyzed during the current study available from the corresponding author on reasonable request.

Code availability

See example code in https://github.com/nlezamaochoa/refugia-bright.

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Author contributions

N.L.O., S.B., H.W., S.B. and E.H. designated the study. N.L.O. performed the analysis and wrote the first version of the manuscript. S.B., H.W. and J.B. provided code and guidance for the methods. J.B., S.B., K.F., B.A., M.P.B., M.J., B.M., O.L., T.C., R.F., D.L., S.B., H.W., S.B. and E.H. coordinated the work and provided technical guidance. All the authors contributed to the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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