RESEARCH ARTICLE

Marine cold-spells in the California Current System: Modeling changes in frequency and impacts on endangered species habitat

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Abstract

Marine cold-spells are an understudied phenomena which can both negatively impact marine wildlife and provide thermal refugia for species displaced by climate change. To develop forward-looking and climate-ready management schemes, it is critical to examine how marine species respond to cold-spells, how long-term warming will affect marine cold-spells over the next century, and how these future cold-spells will in turn affect species of conservation concern, particularly in marine protected areas. To this end, we detect marine cold-spells across the California Current System, a productive Eastern Boundary Upwelling System, relative to a fixed baseline (1980–2009) and to a detrended time series that isolates cold-spells from long-term climate change. We then project the impact of future marine cold-spells on habitat suitability for two endangered top predators: leatherback turtles (*Dermochelys coriacea*) and blue whales (*Balaenoptera musculus*). Models project that 68–99% of the California Current System will no longer experience fixed baseline marine cold-spells by 2099 under a high emissions scenario, though marine cold-spells will still occur relative to a detrended time series. Blue whales lost 5% of their core habitat in National Marine

Sanctuaries during historical marine cold-spells and are projected to gain 1–2% more core habitat during future, fixed baseline marine cold-spells. Leatherback sea turtles had little core habitat change during historical marine cold-spells but are projected to gain 4–5% more core habitat during future marine cold-spells. It is plausible that both species gain habitat during future marine cold-spells because these events provide thermal refugia to their prey. We urge conservationists and ecologists to increase their attention to marine cold-spells as potential thermal refugia and prioritize collecting data on endangered species' prey in order to understand more deeply how species will respond to extreme temperature events.

Introduction

While much research documents the long-term impacts of global climate change on biological systems, a growing body of work emphasizes the importance of acute events [1]. Marine cold-spells (MCSs), defined as discrete periods of anomalously cold sea surface temperature [2], have a wide range of potential impacts on marine organisms, but are understudied relative to marine heatwaves. Extreme MCSs can harm marine species by causing mass wildlife mortality [3,4], decreasing larval survival [5,6], and contributing to coral reef bleaching [7,8]. Cold temperatures also benefit species, particularly in upwelling areas that are associated with high productivity, which can serve as "thermal refugia" from climate change [2,9–12]. Despite observed impacts of discrete MCS events, a standardized method of understanding their impacts on marine ecosystems is lacking. Global-scale analyses show that, when measured relative to a fixed baseline, MCSs have been occurring less frequently [13–15]. However, changes in the location and intensity of MCSs measured relative to changing thermal baselines have received less attention. Given the potentially variable ecological impacts of MCSs, including the ability of species to adapt both to shifting baselines and anomalous events, it is important to predict responses to MCS events which are characterized relative to both a fixed baseline of historical climate ("fixed baseline MCSs") and the long-term warming signal and seasonal cycle ("detrended MCSs").

Information on how MCSs may vary in time and space is critical for habitat conservation decision-making. The most common spatial management tool available to protect key marine habitats are marine protected areas, which regulate human uses of marine areas. Marine protected areas have proliferated globally in recent decades; the area of the global marine protected area network grew 150% between 2012 and 2019 [16].

Marine heatwaves (the reverse of MCSs) are more widely researched than MCSs, likely because marine heatwaves detected relative to a fixed baseline are increasing globally in frequency and duration [14]. Marine heatwaves tend to occur in the summer and fall months, while MCSs are more frequent in the winter and spring [14]. Marine heatwaves are known to redistribute species that marine protected areas are intended to protect (e.g., fish, marine mammals, and sea turtles) [17], but there has been less attention paid to the potential impact of MCSs on marine protected areas.

The California Current System (CCS) is characterized by nutrient-rich upwelling which supports diverse marine mammal, fish, reptile, and seabird populations [18]. The CCS's National Marine Sanctuaries (NMSs) are an example of a robust marine protected area network, which makes the CCS an ideal place to study the impacts of extreme events on habitat in marine protected areas.

We evaluated the impacts of MCSs on the habitat of two endangered species that use the CCS's NMSs: blue whales (*Balaenoptera musculus*) and leatherback turtles (*Dermochelys coriacea*). Both species are classified as Endangered under the US Endangered Species Act [19,20]. Additionally, in the eastern Pacific the blue whale population is categorized as depleted, and the leatherback population is categorized as facing high extinction risk [21,22]. Neither species is at risk of immediate physiological impacts from MCSs given they are adapted to thermoregulate and survive in cold environments [23,24]. However, they are at high risk of interacting with anthropogenic activities (e.g., shipping vessels, fishing gear) if they shift their ranges in response to MCSs. Furthermore, both species are ecosystem sentinels because their movements signal changes in climate and food web dynamics [25]. Finally, leatherback turtles and blue whales provide good case studies of species redistribution in relation to MCS given that robust long-term tracking datasets and extensively validated species distribution models (SDMs) exist for both species [26,27].

Here, we used sea surface temperature data and species distribution models to answer two questions: (1) How will fixed baseline MCSs and detrended MCSs change in the CCS through the 21st century? (2) How will the size of two endangered ecosystem sentinels' habitat change in CCS NMSs during MCSs? This work serves to contextualize MCSs within the backdrop of climate change and contribute to the conservation of two endangered species by understanding how MCSs affect these species' habitats.

Materials and methods

Study area

The CCS extends from Vancouver Island to Baja California [28]. Within the CCS, there are five established NMSs, four of which are located off the coast of California. We chose to focus on the four California coast NMSs because the domain used to predict habitat does not cover the other NMS. Therefore, the NMSs of interest to this study are: Greater Farallones, Cordell Bank, Monterey Bay, and Channel Islands (listed north to south) (Table 1, Fig 1). A sixth NMS, the Chumash Heritage NMS, has recently been designated along the Central California coast [29].

In addition to its robust NMS network, the CCS may provide thermal refugia for heat sensitive species because it is an Eastern Boundary Upwelling System. In Eastern Boundary Upwelling Systems, equatorward winds drive surface offshore Ekman transport, causing deep, cold water to upwell along the coast. Climate change could increase upwelling-favorable winds in some portions of Eastern Boundary Upwelling Systems, while decreasing them in others [34–38], potentially dampening or enhancing the impacts of global warming on a local scale.

A previous analysis of *in situ* observations from the central California coast (between Point Concepcion and Monterey Bay) found that positive upwelling anomalies may play a role in initiating MCS events [39]. In particular, more MCS days

Table 1. Information on National Marine Sanctuaries located off the coast of the California Current System, north to south [29–33].

Sanctuary name	Location (mean latitude)	Ecosystems	Size (km²)
Greater Farallones	Central California coast (38°)	Bays, estuaries, mudflats, marsh, intertidal	8,500
Cordell Bank	Offshore of the San Francisco Bay area (38°)	Deep seafloor and pelagic zone	3,300
Monterey Bay	Monterey Bay, Big Sur coast (37°)	Rocky intertidal, kelp forests, underwater canyon	16,000
Chumash Heritage	Offshore San Luis Obispo, between Monterey Bay and Channel Islands (35°)	Kelp forests, rocky reefs, sandy beaches	17,000
Channel Islands	Coastal Santa Barbara, encompasses remote Channel Islands (34°)	Rocky intertidal, sandy beach, inshore kelp forest, soft bottom, deep-sea coral	3,800

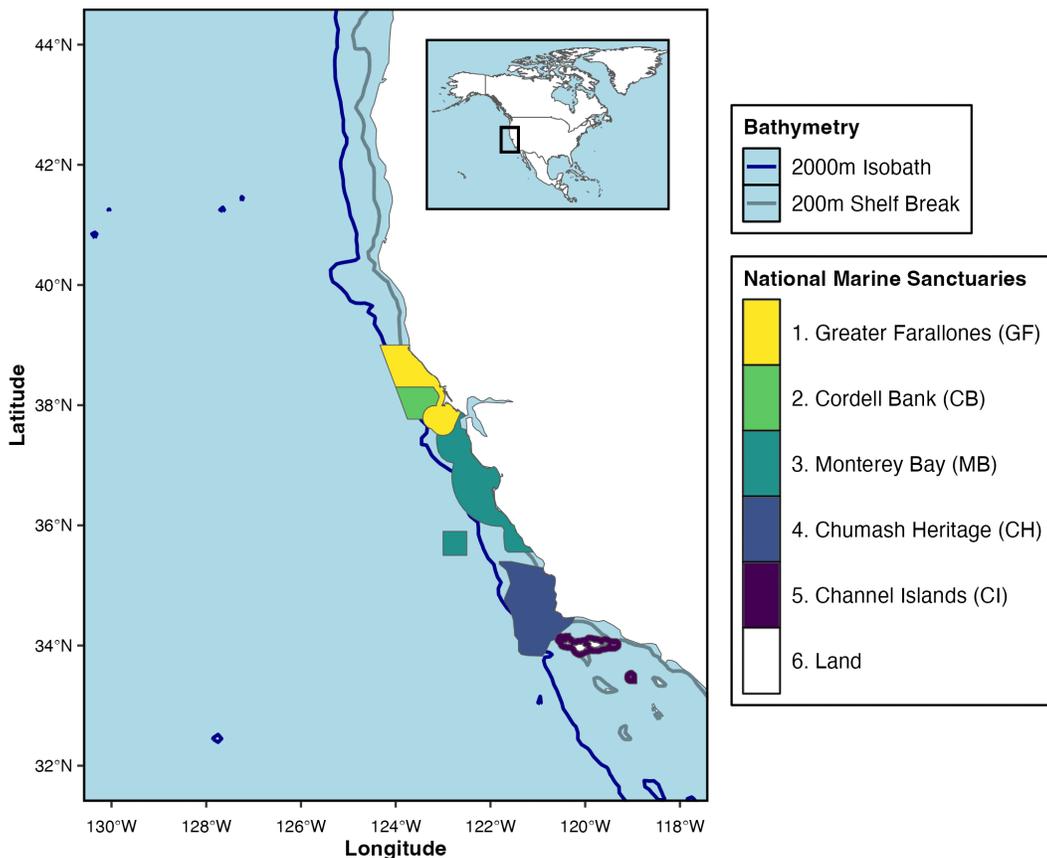https://doi.org/10.1371/journal.pclm.0000563.t001

Fig 1. National Marine Sanctuaries within the California Current System. Basemap was sourced from Natural Earth via the *rnaturalearth()* package in R.

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were observed when cold climate modes (i.e., cold Pacific Decadal Oscillation and La Niña cycles) coincided with positive upwelling anomalies (69% of total MCSs observed occurred during a cold phase of the Pacific Decadal Oscillation simultaneous with a positive upwelling anomaly) [39]. Along the central California coast, oscillations in climate modes and upwelling appear to have been the primary driver of changes in marine heatwave and MCS days over the last four decades (rather than long-term climate change) [39].

Target species

Eastern North Pacific blue whales migrate seasonally between California in the summer and Central America in the winter. They are well documented to shift their habitat during marine heatwaves, which may increase their risk of human encounters [26]. In the last few decades, blue whales have experienced disproportionately high mortality as a result of entanglement in fishing equipment and ship-strikes [25,26,40]. Blue whales feed on krill, for which cold years are generally favorable [41]. Since MCSs are correlated with cold phases in the interannual variability and positive biological upwelling indices [39], MCSs may be favorable for krill and therefore blue whales. An increased understanding of blue whale distributions during extreme temperature events could allow for better protection of these charismatic animals.

Leatherback turtles are the largest species of sea turtle [19]. They are widely distributed and migrate across the Pacific from western Pacific nesting beaches in Indonesia, Papua New Guinea, and the Solomon Islands to foraging grounds in

the northeastern Pacific, including the CCS between April and November [19,42]. Leatherback turtles are mesotherms with thermoregulatory capabilities [23]. They feed on gelatinous zooplankton (e.g., jellyfish, salps, and pyrosomes) and sea nettles [43–45], and their occurrence in the CCS is linked to strong upwelling, which may be favorable for brown sea nettles (*Chrysaora fuscescens*) [46]. Therefore, the effects of MCSs on leatherback turtle prey may be diverse. If their prey respond more positively to strong upwelling conditions, leatherback turtles may be a species for whom MCSs (which correlate to upwelling anomalies) may serve as thermal refugia in the future.

Model types and selection

Modeled sea surface temperature. To define MCSs, we used 0.1° daily resolution sea surface temperature (SST) data. For 1980–2009, we used SST from a regional ocean reanalysis for the CCS [47]. The reanalysis product has been extensively validated in multiple studies and demonstrates significant correlations with remotely sensed and *in situ* surface and subsurface temperature data [47–49]. For example, when compared to *in situ* SST data from six coastal locations, the reanalysis typically exceeded correlation values of 0.80 with some locations reaching correlation values of 0.97 [49]. Furthermore, the CCS reanalysis and its near-real-time counterpart (oceanmodeling.ucsc.edu) are the basis for the authoritative upwelling indices along the US west coast [50,51].

For SST projections starting in 2010, we used previously published downscaled ocean projections; the same CCS model configuration employed in the historical period was forced by output from three earth system models (ESMs) from the fifth phase of the Coupled Model Intercomparison Project (CMIP5) [47]. To reduce bias in the ESM projections, a time-varying delta method was applied to the ESM outputs before running the regional ocean models. For each ESM variable, a time-varying delta was defined as the difference between the ESM change for the whole period (1980–2100) relative to its historical (1980–2010) monthly climatology. The time-varying delta was then added to a realistic historical climatology obtained from atmosphere and ocean reanalysis. The time-varying delta method reduces bias in the downscaled ESM projections by combining observed historical climatologies with long-term variability and change (the time-varying delta) inherited from the ESM [52]. Comparing the historical period of these projections with observations demonstrated that the biases are effectively removed by the time-varying delta method [52]. This method of fitting ecological models on historical reanalyses or other observation-based datasets and then projecting to the future with ocean model output is a standard practice for ecosystem modeling [17,53] provided that biases are consistent between the historical data and the projections, as they are here.

The three ESMs used for the SST projections were: the Hadley Center HadGEM2-ES, Institut Pierre Simon Laplace CM5A-MR, and the Geophysical Fluid Dynamics Laboratory ESM2M. Hereafter, we refer to the three downscaled ESMs as HAD, IPSL, and GFDL, respectively. We chose these three ESMs because they represent a range of potential futures; HAD projects the strongest warming SST anomalies, IPSL projects moderate SST increases relative to the CMIP5 mean, and GFDL projects weaker warming than most CMIP5 models [52]. All ESMs were forced under the high-emission Representative Concentration Pathway (RCP) 8.5 scenario [52]. There is more variability across CMIP5 models for one given RCP than there is variability for one model across all RCPs. RCP 8.5 encompasses the high end of potential climate impacts as well as possible outcomes that fall within lower RCP scenarios (for example, GFDL under RCP 8.5 has similar warming to the CMIP mean under RCP 4.5).

We performed the cold-spell and habitat projections on each of the three downscaled ESMs separately and then averaged the three sets of projections.

Species distribution models. SDMs relate species occurrence data or abundance to concurrent environmental conditions to determine which environmental factors drive patterns of distribution [53]. SDMs are widely applied to understand the spatio-temporal ecology of a species [53–55]; numerous studies use SDMs to quantify species responses to extreme temperature events and project their distributions under climate change [17,56–58]. Both SDMs used here predict habitat suitability from a variety of environmental variables as well as one fixed spatial variable (bathymetry).

We used a blue whale SDM built by Abrahms et al. [26] using satellite tracking data for 104 blue whales from 1994 to 2008. Abrahms et al. [26] developed two generalized additive mixed models, one which described whale habitat in winter/spring (during northward migration) and one that described habitat in summer/fall (during southward migration). Here, we exclusively used output from the summer/fall model since that is when blue whales spend the most time in the CCS [26]. The model had high predictive performance on the original dataset and on an independent sightings dataset consisting of 3,413 observations (Area Under the receiver operating Curve (AUC) = 0.908; True Skill Statistic (TSS) = 0.755) [26].

We used a leatherback turtle SDM built using satellite tagging data from the period 2001–2020 [27]. The leatherback turtle SDM was fitted using boosted regression trees that were spatiotemporally validated by Lezama-Ochoa et al. [27]. Unlike for blue whales, the leatherback SDM is not unique to one season. The model demonstrated high accuracy in all validation tests [27].

Ethics statement. All satellite tagging data used to build the blue whale and leatherback SDMs were collected for the purposes of prior studies [26,27]. Blue whale tagging in the United States was authorized by the National Marine Fisheries Service under permit numbers 841 (1993–1998), 369–1440 (1999–2004), and 369–1757 (2005–2010), and tagging in Mexico was authorized by the Secretarìa de Medio Ambiente y Recursos Naturales, Mexico (permit number DOO 028319 and SGPA/DGVS 0576). The Oregon State University Animal Care and Use Committee also approved the blue whale tagging. Leatherback tagging was conducted under Endangered Species Act permit nos. 15634 and 21111.

Habitat prediction. The variables that contributed most to the SDMs were SST and bathymetry (S1 Table). In the leatherback model, SST was the most important variable, followed by bathymetry. In the blue whale model, bathymetry was the most important variable, followed by the standard deviation of sea surface height, SST, and isothermal layer depth. Habitat suitability (hereafter habitat) values describe potential species habitat.

We used environmental data from the dynamically downscaled climate models (in section "Modeled sea surface temperature") to project species habitat suitability across the CCS from 1980-2099. Because the SDMs used the same modeled SST values that were used to identify cold-spells, we could say that the modeled habitat values were responding to the same temperature shifts we detected in the modeled cold-spells.

Model interpretation

Marine cold-spell detection. We defined MCSs as periods for which SSTs fall below the 10th percentile for a given climatological mean for at least five days (Fig 2) [2]. We detected MCSs for each 0.1° grid cell in the CCS from 1980 to 2099 for each of the three downscaled ESMs in order not to lose the temperature variability expressed in the models by averaging them.

We used the "heatwaveR" package in R [59] to detect MCSs for each baseline, model, and grid cell combination. HeatwaveR was developed for the purpose of detecting marine heatwaves and was modified for our purposes to flag SSTs which fall below the threshold for more than five days as MCSs (gaps of one or two days without MCS conditions are included but not gaps of more than two days). HeatwaveR generates metrics for each MCS detected (S2 Table).

MCSs were defined in two ways. First, we detected MCSs using a fixed baseline based on the 1980–2009 seasonal climatology according to Hobday et al.'s definition [60,61]. We used the 1980–2009 window to define our fixed baseline here because it is the standard for large-scale MCS analyses [59]. In this case, the threshold for a MCS was defined as the 10th percentile of sea surface temperatures modeled for a given day of the year. The fixed threshold reflects seasonal variability because it is defined relative to daily mean temperatures.

Second, we detected MCSs relative to long-term trends. To do so, we first removed seasonally-dependent long-term trends from our SST time series. Removing seasonally-dependent trends is important because the seasonal cycle in SST is projected to increase in the future; if a single (not seasonally-dependent) trend is removed, the changing seasonal cycle will be incorrectly characterized as increased internal variability. For each day of the year, we calculated a quadratic fit to the SST time series (e.g., the January 1 regression was fit to 120 SST values observed on January 1 of each year
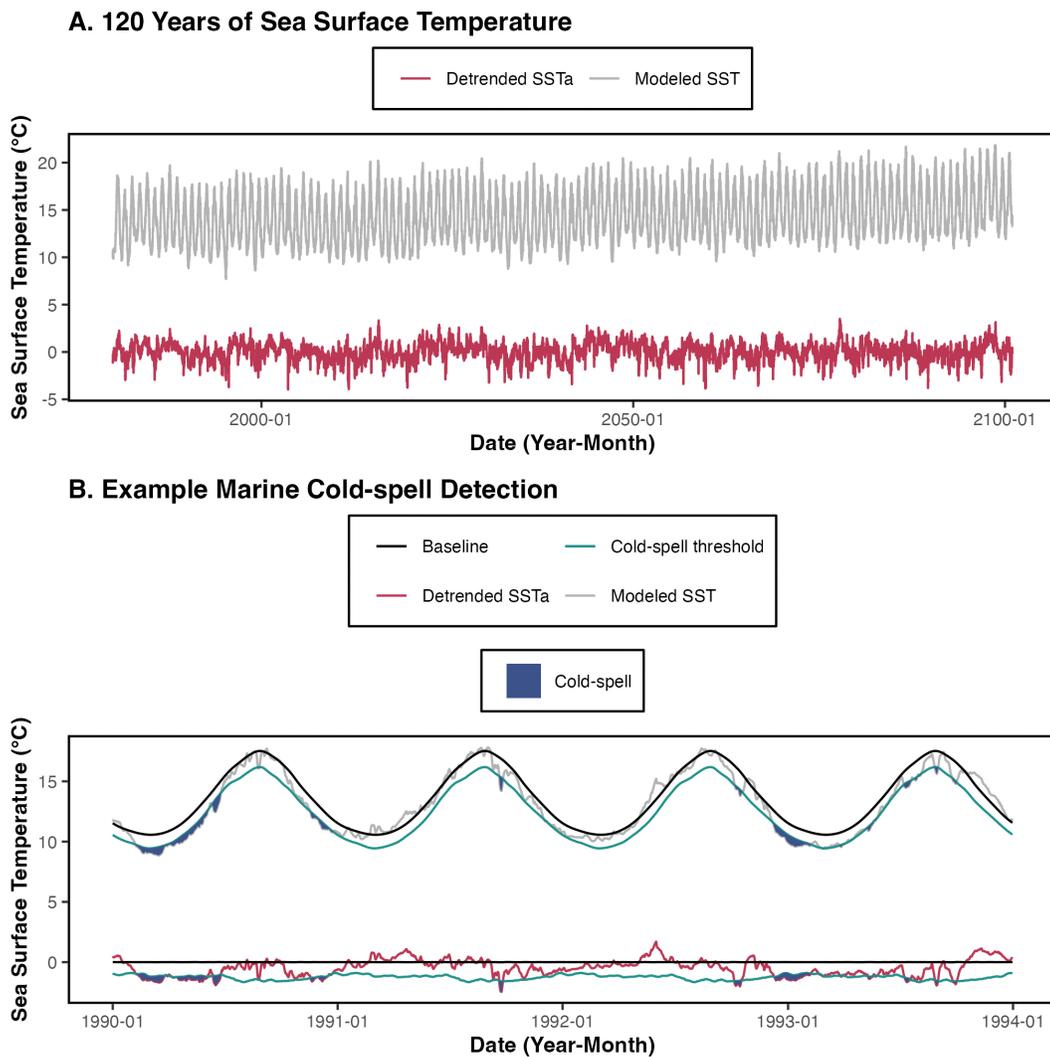
A. 120 Years of Sea Surface Temperature

B. Example Marine Cold-spell Detection

Fig 2. Examples of marine cold-spell detection methods. A displays 120 years of modeled sea surface temperature (dynamically downscaled from the Geophysical Fluid Dynamics Laboratory ESM2M) and detrended time series (calculated by subtracting predictions from daily, quadratic regressions of SST) for a grid cell in Monterey Bay. **B** displays marine cold-spell detection from the ensemble sea surface temperature and the anomaly during a four year period. Sea surface temperatures and anomalies that fall below their respective thresholds (represented by light blue lines) for more than five days are defined as marine cold-spell events.

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throughout the dataset). This quadratic fit was then removed from the raw SST to obtain detrended SST values. Finally, MCSs were detected from the detrended time series using the same procedure as described above for fixed baseline MCS. Our detrending method enabled us to view temperature anomalies independent of both the long-term mean trend and seasonal cycles. Similar to the fixed baseline case, the threshold for a MCS was the 10th percentile of modeled anomalies for each day of the year.

By using both fixed and detrended methods, we could explore the impacts of the total temperature change (fixed baseline MCSs) as well as the impacts of temperature variability relative to a shifting mean state (detrended MCSs) [62]. As there is a lack of consensus on whether long-term trends should be removed for detection of temperature extremes [49,62–64], and each approach has different ecological implications, we report results for both definitions of MCSs.

We examined changes in MCSs on both the CCS scale and the NMS scale. On the CCS scale, we compared historical MCSs (1980–2009) to future MCSs (2070–2099) by finding the total number of MCSs for each grid cell of the CCS during each thirty-year period. We chose thirty-year windows for our broad-scale analyses because thirty-year windows have been shown to encompass internal climate variability [65]. On the NMS scale, we computed the annual average per decade of the following MCS metrics: average number per year, average duration, average days per year, and average intensity (temperature anomaly) for both fixed baseline and detrended methods (S2 Table). We performed these calculations for MCSs in NMSs because we wanted to better understand how MCSs will change in these key habitats in the future.

Changes in habitat. The SDMs produce continuous habitat estimates ranging from one (most suitable) to zero (least suitable). To identify core habitat, we used the "equal sensitivity/specificity threshold," which balances the model's ability to detect presences and absences (i.e., the True Positive Rate and True Negative Rate are equally optimized) [17,66]. Core habitat for both blue whales and leatherbacks was defined as any grid cell with a habitability score greater than 0.50.

We measured core habitat in 0.1° grid cells. We compared the core habitat available to each species during MCSs (MCS_CORE) to the monthly average core habitat available over the decade (µCORE). We measured changes in core habitat (ΔCORE) as the percent change in grid cells relative to the size (i.e., the number of grid cells) of a given NMS ($CELLS_{NMS}$) according to the following equation:

$$\Delta CORE = ((MCS\_CORE - \mu CORE)/CELLS_{NMS})*100$$

We found the µCORE by averaging the core habitat available for each month when our species occupy the CCS (July through October for both species) for each decade of the study period. During the months of November to June, both species had very little core habitat available in the CCS, so analysis of habitat response to MCSs would have been representative of a hypothetical, small population of animals. Furthermore, the SDM had fewer points from the winter and spring seasons for both of the species (S3 Table), so the models could not be as certain about the species' habitat during these times.

We found MCS habitat conditions by averaging the number of grid cells of core habitat available during each day of the MCS. We compared fixed baseline MCSs to typical conditions for our species between 1980 and 2009 (the standard fixed baseline) [59]. We compared detrended MCSs to a sliding window of contemporaneous typical conditions. To reduce noise in the typical conditions, we compared each MCS to typical conditions averaged from three decades (e.g., a Channel Islands MCS centered around July 10th, 2030 was compared to a mean of Channel Islands typical conditions from July 2020, July 2030, and July 2040). MCSs occurring during the 1980s were compared to a mean from 1980 and 1990 and MCSs occurring during the 2090s were compared to a mean from 2080 and 2090.

Finally, we averaged the change in core habitat size during MCSs for every decade to understand how species may have been responding differently to MCSs through time. We performed these analyses with MCSs detected using both a fixed baseline and the detrended method. Similar analyses of change in core habitat have been used to understand the effects of marine heatwaves on marine predators [17].

Response curves. Our habitat results can be explained by the SDM response curves to SST. To aid in interpreting our habitat results, we calculated the blue whale SDM summer/fall model response curve to SST (and 95% confidence interval) and the leatherback SDM response curve to SST. We overlaid density curves of SST used to calculate habitat response during two decades of MCSs in the Monterey Bay NMS (for simplicity, we focused exclusively on Monterey Bay). All SSTs shown in the figure are modeled by an ensemble of predictions from the IPSL, GFDL, and HAD CMA5A-MR RCP 8.5 models.

Results

Changes in marine cold-spells by 2099

Marine cold-spells across the study area. During the historical period (1980–2009), we found an average of 28 fixed baseline MCSs days per grid cell per year in the CCS (Fig 3A). Under a high emissions scenario, fixed baseline MCS
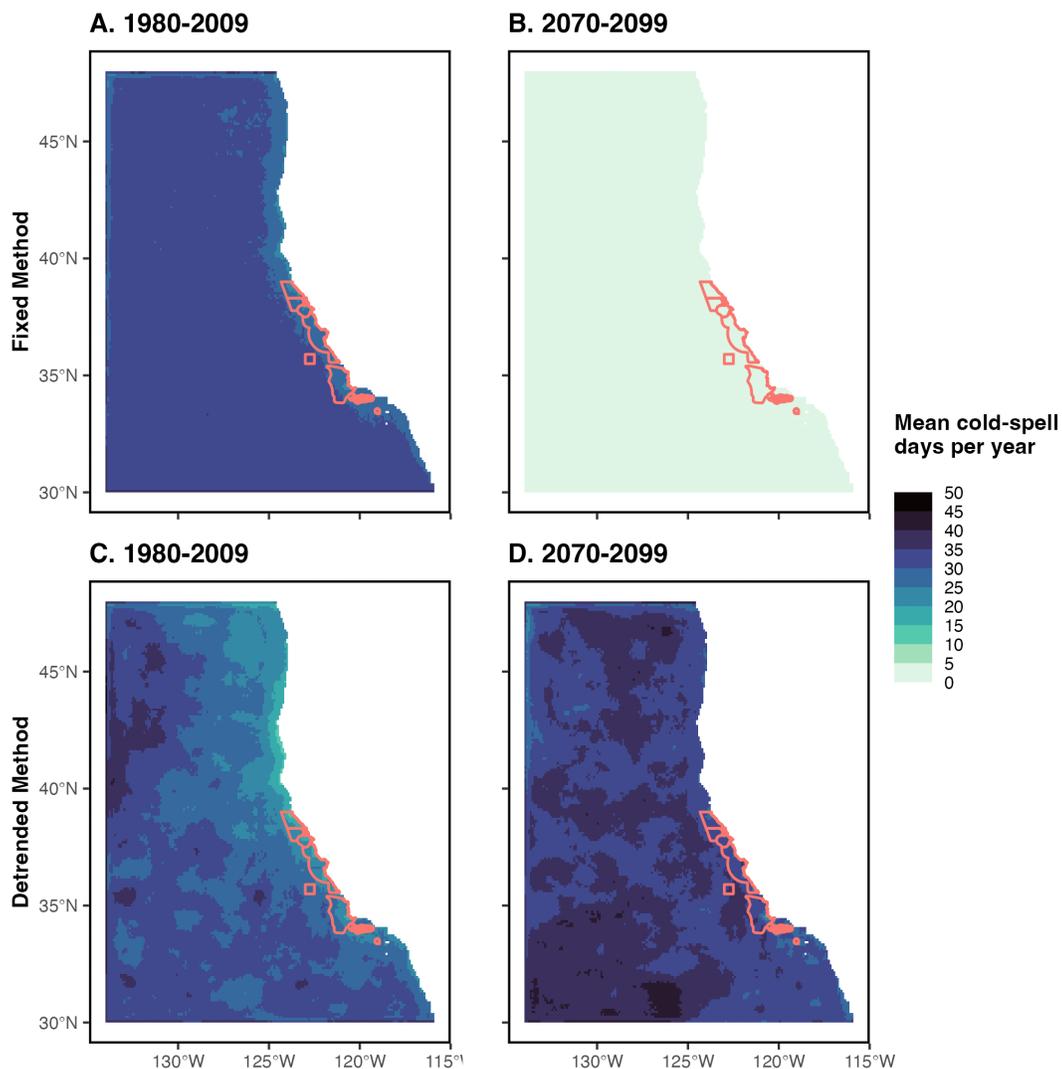
Fig 3. Projected change in marine cold-spells in the California Current System from the historical period (1980-2009) to the future period (2070-2099). **A** and **B** display ensemble mean projections of the average number of fixed baseline marine cold-spell days per year across the three climate models. **C** and **D** show projections of the average number of detrended marine cold-spell days per year across the three climate models.

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days were projected to decrease dramatically everywhere in the CCS (Fig 3B). Of the three models, GFDL projected the coldest SSTs in 2099, but it still projected that 68% of the CCS will experience no fixed baseline MCSs during the future (2070–2099) period. IPSL and HAD both projected that 99% of cells would experience no fixed baseline MCSs in the future period (S1 Fig).

In the three models examined here, the total number of days of detrended MCSs was projected to increase in the future relative to the historical period by an average of 2.5 MCS days per grid cell (Fig 3C and 3D), although these increases may be driven by multi-decadal variability.

Marine cold-spells in National Marine Sanctuaries. All five NMSs were projected to experience rapid declines in total yearly fixed baseline MCS days (Fig 4A). In 1980, NMSs typically experienced an average of 28.1 fixed baseline
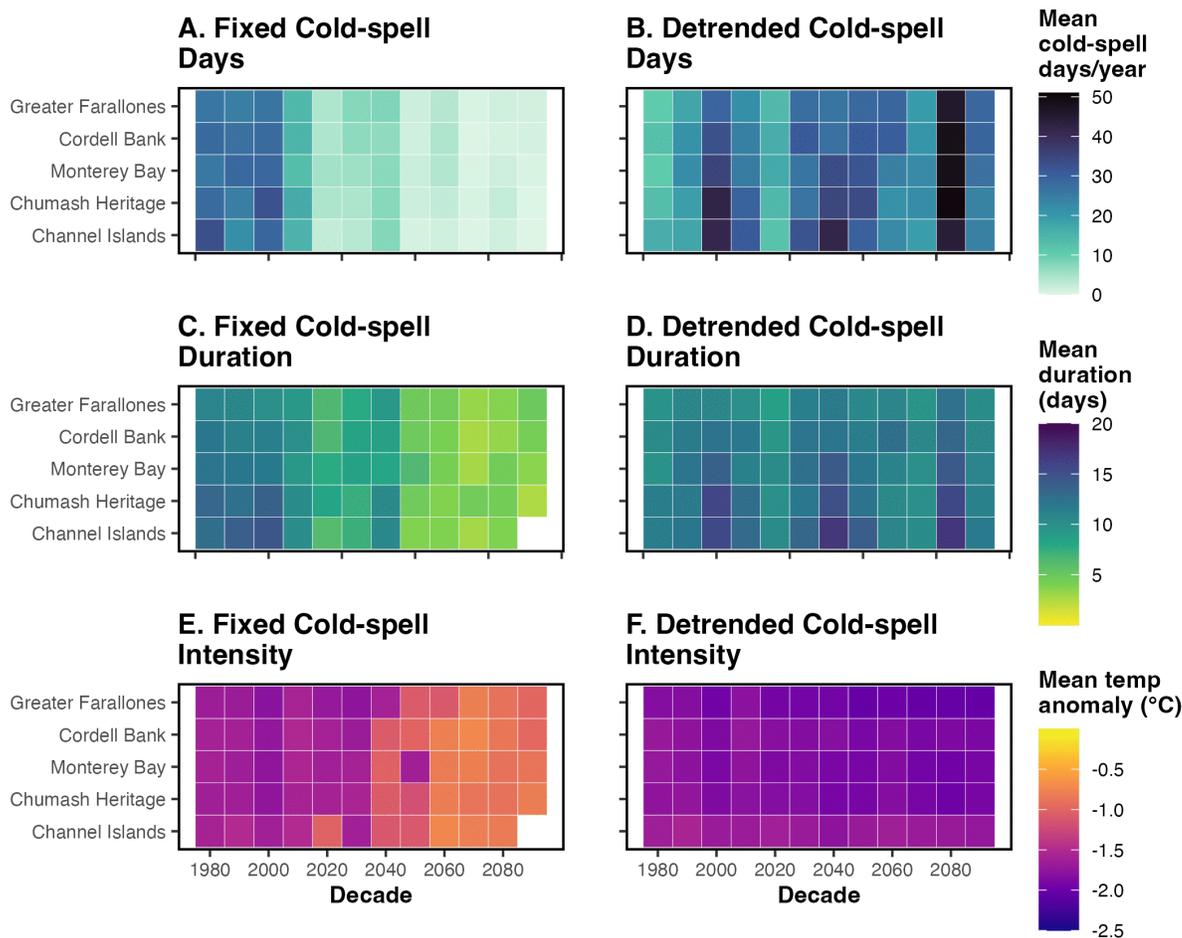
Fig 4. Projected changes in marine cold-spells within California's National Marine Sanctuaries. A, **C**, and **E** show changes in fixed baseline marine cold-spells. **B**, **D**, and **F** show changes in detrended marine cold-spells. All plots show decade on the x-axis and National Marine Sanctuary name (ordered North to South) on the y-axis. **A** and **B** are colored by the mean number of cold-spells per year. **C** and **D** are colored by the mean cold-spell duration in days. **E** and **F** are colored by the average difference between typical sea surface temperatures and sea surface temperatures during marine cold-spell events. All metrics are calculated for each model individually and then three models are averaged. All metrics for the Channel Islands in the 2090s are zero for fixed baseline marine cold-spells because no fixed baseline marine cold-spells were detected in this sanctuary during this time.

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MCS days per year. In 2090, the models projected that NMSs will witness a rapid decline of fixed baseline MCS conditions to an average of 0.5 fixed baseline MCS days per year (Fig 4A). Duration and intensity (mean temperature anomaly) of fixed baseline MCSs will also decrease (Fig 4C and 4E).

Models did not project an increase or decrease in the number of detrended MCS days per year over the course of twelve decades, although there were signals of strong multi-decadal variability in MCS days per year (Fig 4B). The duration of detrended MCSs in NMSs did not change (Fig 4D). The Channel Islands NMS had relatively less intense detrended MCSs than the four other NMSs (Fig 4F).

Habitat changes

Habitat across the study area. Before analyzing the species' habitat responses to MCSs, we considered broad scale changes in species habitat across the CCS during the study period (Fig 5). Blue whales were projected to lose
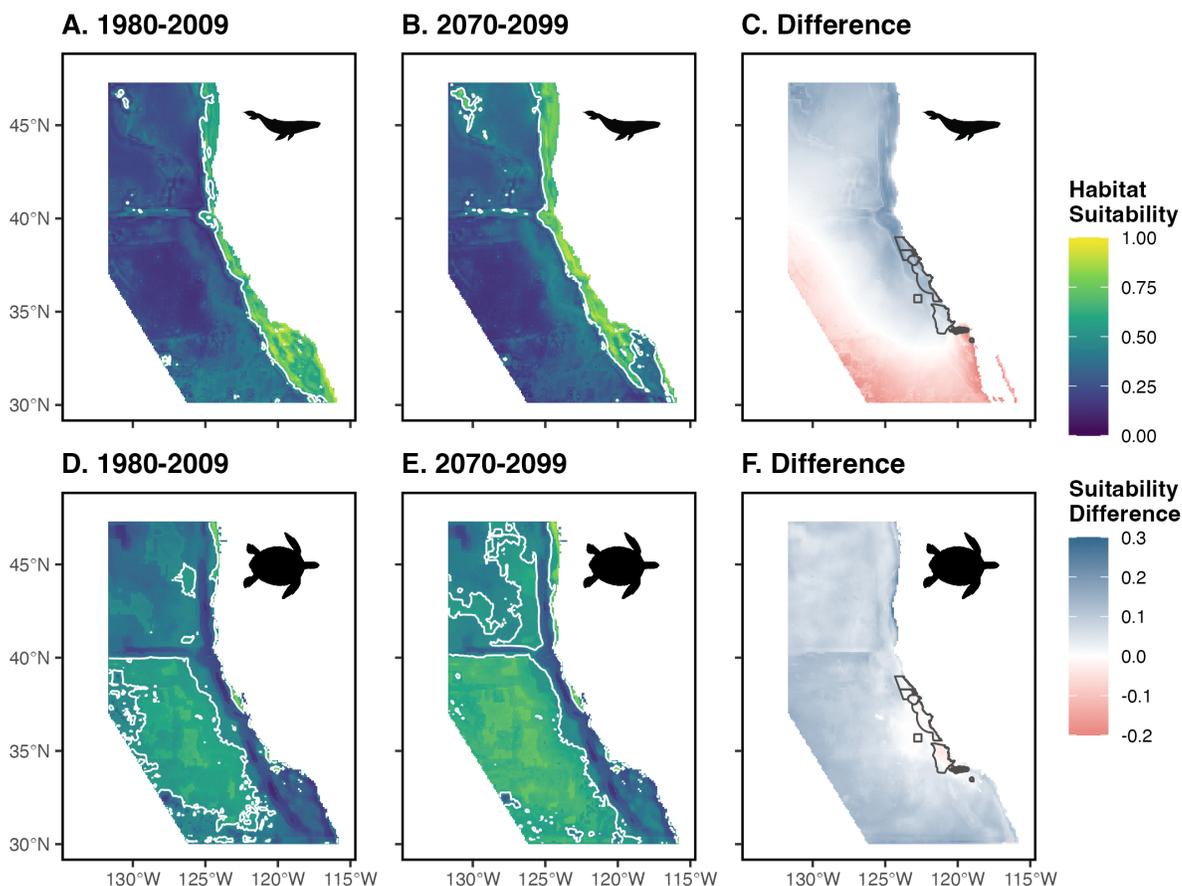
Fig 5. Projected change in blue whale and leatherback sea turtle core habitat in the California Current System from the historical (1980-2009) to the future (2070-2099). **A, B, D,** and **E** display average predicted habitat suitability values (across ESMs) for these species from July to October, when these species migrate to the California Current. Habitat suitability values of one (yellow) indicate a high likelihood of species presence while values of zero (dark blue) indicate very low chances of species presence. Core habitat for each species is outlined in white. **C** and **F** display the differences between historical and future habitat suitability values (future minus historical period) with National Marine Sanctuaries outlined in black where blue represents gain of core habitat and red represents loss of core habitat.

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core habitat in the southern CCS, particularly along the coast, and gain habitat in the central and north CCS (Fig 5C). Leatherbacks were projected to gain core habitat across the CCS.

Habitat in National Marine Sanctuaries. Blue whale response to MCSs varied by latitude. In mid-latitude NMSs (Cordell Bank, Monterey Bay, and Chumash Heritage), blue whales experienced decreasing core habitat size during both fixed baseline and detrended MCSs (Fig 6A and 6C); blue whales lost 5% of their core habitat in NMSs during both fixed baseline and detrended MCSs (Table 2). In the future, blue whales had positive or little habitat response to fixed baseline and detrended MCSs (Fig 6A and 6C). However, blue whales gained core habitat during fixed and detrended MCSs in the Greater Farallones and had little habitat response to fixed and detrended MCSs in the Channel Islands (Fig 6A and 6C).

Leatherbacks' response to MCSs also varied by latitude, but this variability was less defined than for blue whales. Leatherbacks had mixed responses to historical MCSs (both fixed baseline and detrended events) and to future MCSs in northern NMSs (Fig 6B and 6D). In southern NMSs, leatherbacks gained core habitat during future fixed and detrended MCSs in the future, although this pattern was more pronounced for detrended MCSs, during which leatherbacks gained an average of 5% more core habitat (Table 2).
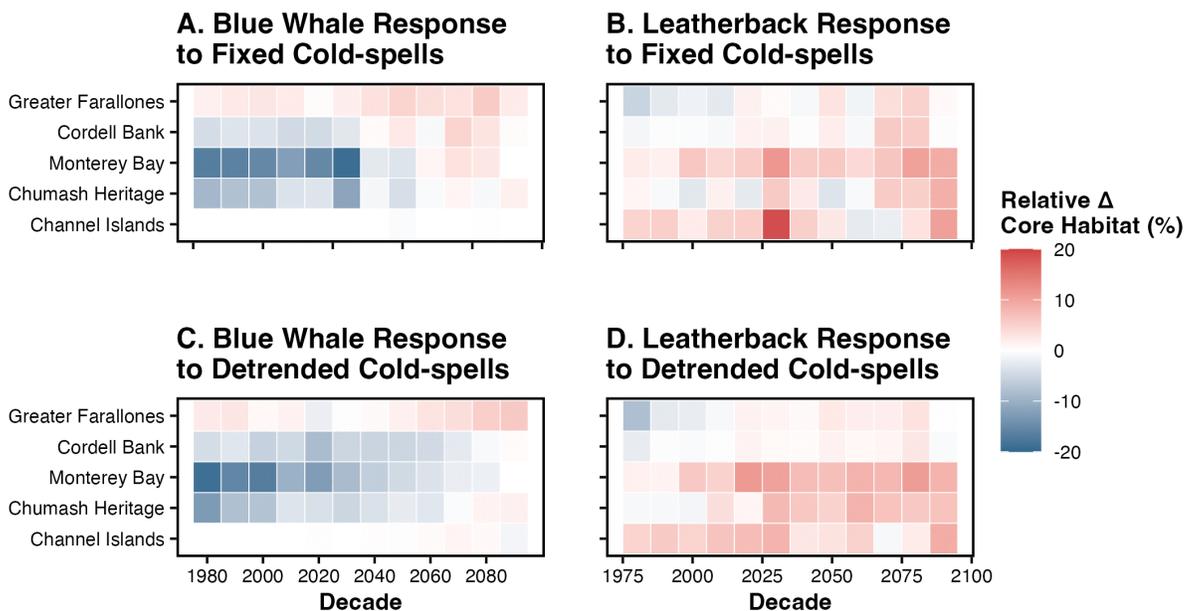
Fig 6. Projected change in core habitat for blue whales and leatherbacks during July-October marine cold-spells in National Marine Sanctuaries. For each plot, columns represent twelve decades of data and rows represent each of the five National Marine Sanctuaries in latitudinal order. The color fill in each cell represents the relative percentage change of core habitat available to the study species during marine cold-spells relative to typical conditions (calculated as the change in core habitat available divided by the size of the National Marine Sanctuary). For fixed baseline marine cold-spells, typical conditions are defined as the period between 1980 and 2009. For detrended marine cold-spells, typical conditions are defined as a three-decade sliding window of contemporaneous conditions (except for marine cold-spells occurring in 2080 and 2090, when typical conditions are defined by a two-decade window). **A** and **C** display changes in blue whale core habitat while **B** and **D** display changes in leatherback core habitat. **A** and **B** show the species' responses to fixed baseline marine cold-spells and **C** and **D** show responses to detrended marine cold-spells.

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Table 2. Mean changes in blue whale and leatherback core habitat in National Marine Sanctuaries during marine cold-spells from the historical and future periods. The historical period is defined as 1980-2009 and the future period is defined as 2070-2099. Habitat changes are averaged across five National Marine Sanctuaries and three downscaled ESMs.

Species	Mean *historical* change (%) during *fixed* cold-spells	Mean *historical* change (%) during *detrended* cold-spells	Mean *future* change (%) during *fixed* cold-spells	Mean *future* change (%) during *detrended* cold-spells
Blue whale	-5.15	-5.82	1.75	0.69
Leatherback sea turtle	0.54	0.35	5.13	4.30

https://doi.org/10.1371/journal.pclm.0000563.t002

Standard deviations were measured between habitat responses to distinct MCS events before these responses were averaged to create decadal means (S2 Fig). Standard deviations of blue whale habitat response in the Channel Islands NMS were smaller, while standard deviations of blue whale habitat response in mid-latitude NMSs were larger. Leatherback habitat responses had higher standard deviations during detrended MCSs, particularly in southern NMSs. Large standard deviations indicated that MCSs have a variety of effects depending on their intensity, season, duration, and potentially other factors. Therefore, our averaged habitat results did not dictate MCS impacts, although the results could give us a sense for trends. Trends in MCSs effects are particularly elucidating when we consider MCSs as potential thermal refugia for our species and their prey.

Model mechanisms explain habitat predictions. Our predicted changes in core habitat were explained by species SST preferences, as indicated by the models' response curves (Fig 7). SST was the most influential non-static environmental variable in both the blue whale and leatherback turtle SDMs [35,49]. Blue whale habitat suitability generally
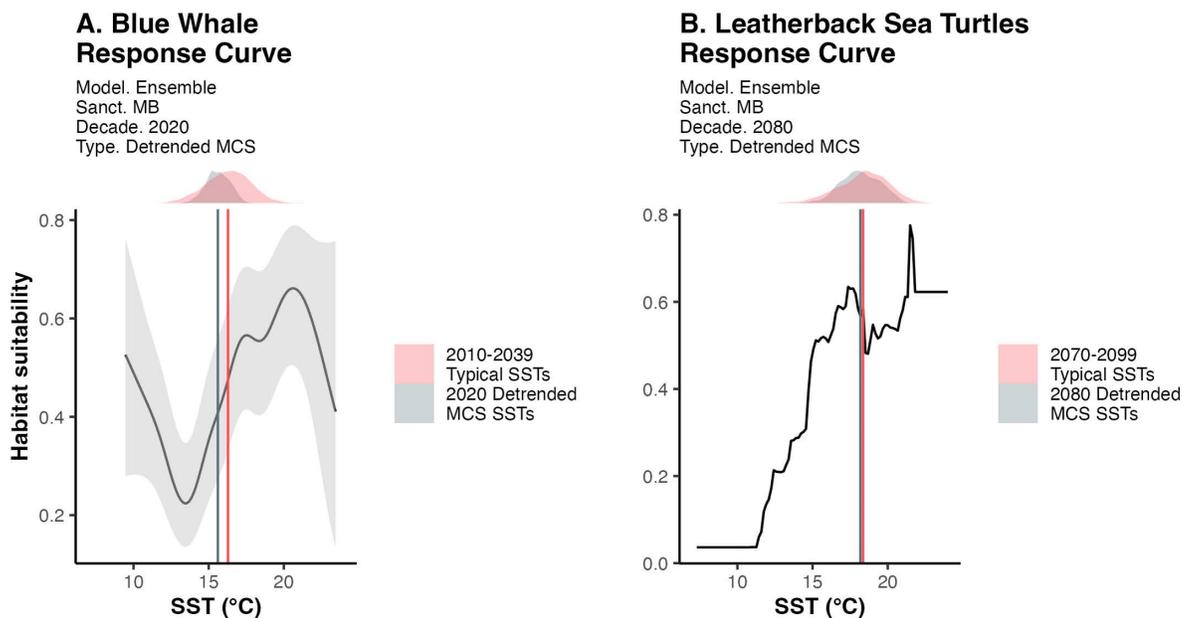
Fig 7. Blue whale and leatherback sea turtle modeled response curves to sea surface temperature modeled across two different periods for the Monterey Bay National Marine Sanctuary. A displays blue whale summer/fall model response curve (black line with 95% confidence interval in gray) and **B** displays the leatherback turtle response curve. Horizontal straight lines in the leatherback turtle model response curve represent an extrapolation from the model response at the lowest or highest observed sea surface temperatures. The density plot on **A** displays sea surface temperatures used to calculate habitat response to marine cold-spells between 2020-2029 in Monterey Bay; the density plot on **B** displays sea surface temperatures used to calculate responses between 2080-2089. Red density curves are sea surface temperature modeled during a thirty-year window surrounding the decade of interest and blue density curves are sea surface temperatures occurring during modeled, detrended marine cold-spells during the decade of interest. Vertical lines represent mean typical (red) and marine cold-spell (blue) temperatures. Sea surface temperatures are derived from an ensemble of the downscaled projection forced by the IPSL, GFDL, and HAD CMA5A-MR RCP models under the RCP 8.5 scenario.

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increased with SSTs from around 13°C-21°C. Below 13°C, habitat suitability increased, and above 21°C, habitat suitability declined. Leatherback turtle habitat suitability generally increased with SST from around 14°C-16°C and became variable from 16°C-24°C. These results have been corroborated by preliminary fine-scale habitat density models developed for leatherbacks in the Monterey Bay and Greater Farallones NMSs [64]. Here, we show two examples of how the response curves can explain our habitat results in the Monterey Bay NMS.

Example a: Blue whales' habitat response to detrended MCSs in the Monterey Bay NMS in 2020. Blue whales lost habitat during detrended MCSs in Monterey Bay in 2020 because these conditions were less suitable than the typical SSTs for this period (2010–2039) (Fig 7A).

Example b: Leatherback turtles' habitat response to detrended MCSs in the Monterey Bay NMS in 2080. Leatherback turtles gained habitat during detrended MCSs in Monterey Bay in 2080 because these conditions were more suitable for turtles than the typical SSTs for this period (2070–2099) (Fig 7B).

Discussion

Here, we examined future changes in MCSs and their effects on two endangered species. We found that under a high emissions scenario, fixed baseline MCSs were projected to greatly decrease and may even cease to exist in the CCS by 2099. While a few MCSs may continue to occur in areas with strong coastal upwelling, this upwelling cannot override the warming effects of climate change (Fig 3).

Blue whales and leatherback turtles had variable responses to MCSs, although both species had increasingly positive responses to MCSs over time (Fig 6). Fixed baseline MCSs were projected to become less intense in the far future (Fig 4) and will therefore represent more mild SSTs and which may be closer to the species' ideal temperature range than historical fixed baseline MCSs. Detrended MCSs were detected relative to temperature anomalies, so these events were projected to represent warmer SSTs in the far future, which may be more representative of the species' ideal temperature range than the "typical" temperatures for the far future (Fig 7). Previous fixed baseline extreme temperature analyses agreed that warming signals tend to overwhelm changes in variability [15,67,68].

Blue whale responses to both fixed baseline and detrended MCSs differed in the furthest north and south NMSs (Fig 6A and 6C). In the Greater Farallones, blue whales had a weakly positive habitat response to fixed baseline and detrended MCSs, possibly because SSTs in the Greater Farallones are colder than mid-latitude NMSs (e.g., Cordell Bank, Monterey Bay, and Chumash Heritage) [69] and these cold SSTs fell on a part of the blue whale response curve where there was a negative relationship between SST and habitat suitability. This part of the response curve plausibly described the positive relationship between cold temperatures and strong upwelling in certain blue whale foraging grounds (e.g., the Greater Farallones). However, the high suitability at SSTs below 13°C was associated with a large confidence interval (Fig 7A). In the Channel Islands, blue whales had very weak habitat response to fixed baseline and detrended MCSs, perhaps because MCSs in this NMS were relatively less intense (Fig 4E and 4F), likely due to weaker upwelling-related variability and the warm influence of the Davidson Current [70]. Furthermore, SSTs in the Channel Islands may be well within the suitable range for blue whales, so MCSs may remain within this range of suitability.

Leatherback turtles had weak responses to fixed baseline and detrended MCSs in the late twentieth century, likely because SSTs in the CCS fell within a suitable range for leatherback turtles in the historical period. Leatherback turtles' responses to fixed baseline and detrended MCSs were projected to become positive, particularly in southern NMSs, towards the end of the twenty-first century (Fig 6B and 6D). Leatherback turtles' shift to positive habitat responses to MCSs indicated that SSTs in the far future may be warmer than the suitable range for leatherback turtles and MCSs may provide them thermal refugia from both typical temperatures and marine heatwaves. Thermal refugia may be more pronounced for leatherback turtles in the Channel Islands NMSs because SSTs are generally warmer [70].

While we cannot determine which habitats species will occupy during extreme temperature events, our results indicated the potential habitat available to species during these events.

Implications for oceanography and ecology

Extreme temperature events detected relative to a fixed baseline will change radically in their frequency, duration, and intensity by the end of the century. In the case of MCSs, events detected relative to a fixed baseline may be so rare in 2099 that they are almost irrelevant. Fixed baseline marine heatwaves, on the other hand, may become so common by 2099 that they cease to describe discrete events [63]. While fixed baseline extreme temperature events are important indicators of warming, these events diverge greatly in frequency of occurrence between the historical and future periods.

A detrended detection method may bring trends in extreme temperature events to light, allowing for a better understanding of impacts from transient vs. persistent warming [71]. For species with thermoregulatory capabilities like those studied here, a detrended method may be more biologically relevant, as it indicates environmental conditions that are beyond what the species normally experienced. Both species had more positive responses to future detrended MCSs than to historical detrended MCSs. These positive late-century responses may have been due to MCSs falling more within the suitable range of temperatures for the species than typical late-century temperatures. In this way, future detrended MCSs may provide some thermal refugia to these two endangered species.

While ecologists regularly use SDMs to predict species response to past and present environmental conditions [17,58], as well as mean future conditions [56,72,73], few studies have used SDMs to model species response to discrete future extreme events. Understanding how species will respond to a changing climate–particularly a new regime of extreme

temperature events–is essential to proactive conservation policy. Here, we identify several considerations in the SDM method for extrapolating species response to extreme temperature events.

First, we note that the SDM model type will affect predicted species responses to extreme events. Boosted regression trees often have jagged response curves while generalized additive models have smoother response curves, so generalized additive models may be better at predicting gradual changes in species response to minor temperature changes [74]. Second, we note that models are best at predicting environmental conditions represented in training data. Therefore, SDMs will be less skillful at predicting species responses to extreme events which fall outside of the precedent range of temperatures [75]. Finally, SDMs cannot incorporate species memory of and fidelity to historic foraging areas, which may limit range shifts in response to slow climate change [76].

Implications for conservation policy

For the purposes of this section, we focus exclusively on our fixed baseline MCS results, as this method provides the most established and therefore most accessible results for policy applications.

The few MCSs our models detected in the future period were clustered along the coast, likely due to mitigated warming—particularly in one model (GFDL) that detected enough events to demonstrate a spatial trend. The projected concentration of fixed baseline MCSs along the coast partially supports previous findings that Eastern Boundary Upwelling Systems may act as thermal refugia [9–11]. Species–particularly longer-lived animals–are unlikely to evolve adaptations to extreme events within decadal timescales [77], so measuring future change relative to historical norms has ecological value. While phenotypic plasticity may buffer species resilience to unfavorable conditions [78], this plasticity may have bounds. Therefore, scientists should continue to prioritize strong upwelling systems via study and NMS designation because these systems may mitigate climate-driven warming trends. However, we ought not assume that simply because an area has strong upwelling, this area will be entirely resistant to climate change; the models still predict that the California coast will lose most of its MCS events, including in the NMSs.

In addition to our findings on CCS refugia, this study provides a broad view of how the habitats of two endangered species may shift in the CCS. Our predictions of habitat suitability values for these species do not indicate whether the species will thrive in the future. Future species distributions will also depend on overlap and mismatch with future prey distributions, which are not incorporated into our SDMs. Both blue whales and leatherback turtles face anthropogenic threats that have pushed them to endangerment [19,24,58,79]. Accurate predictions of these species' distributions can help reduce human-wildlife conflict by providing fishing vessels and ships with foresight on likely species locations. Our results may help conservationists set effective priorities to protect these species.

As climate change warms the CCS, however, optimal blue whale habitat will likely shift further north to areas with SSTs more similar to the historical southern coast. While blue whale migration correlates with an SST gradient [76], studies of blue whale thermoregulation disagree on whether energy conservation is a significant driver of migration [24,80]. More recent studies have found that prey availability is a primary driver of migration patterns [76,81]. Blue whales are krill obligates, and krill biomass has been correlated to cold SST anomalies [81]. As the CCS warms, krill biomass will be larger earlier in the year when waters are colder; this change in krill timing has already led to blue whales arriving earlier in the CCS [81]. Future efforts to conserve blue whale habitat should focus on areas with high krill biomass.

Leatherback turtles tended to gain core habitat across the CCS with climate change. They have been shown to maintain warm body temperatures in cold water and dive to thermoregulate in warm waters [43,44]. Leatherback's primary prey in the NMSs (Pacific sea nettles) may respond positively to cold upwelling years [42], indicating that future MCSs may be providing thermal refugia to leatherback prey in the NMSs. Therefore, prey availability will likely be the primary driver of leatherback turtle habitat in the future. Similarly to blue whales, future research should increase the focus on leatherback turtle prey availability. While this paper contributes to the field of extreme temperature event detection and provides a novel analysis of the effects of MCSs on endangered species, we cannot say with certainty why large species

may behave in certain ways until we understand more fully the response of their prey to extreme temperature events. This work contributes to the future protection of two endangered species by improving our understanding of how these species will respond to MCSs as the climate changes.

Supporting information

S1 Table. Relative importance of environmental variables to species distribution models. Relative importance to the GAM was calculated using the *gam.hp()* package in R and relative influence to the BRTs were calculated using the *summary.gbm()* package in R. BRT relative importance is measured in percent contribution to explained deviance and GAM relative importance is equal to the individual R^2.
(DOCX)

S2 Table. Cold-spell metrics.
(DOCX)

S3 Table. Summer/fall (July-October) versus winter/spring (November-June) presence data points used to build species distribution models. Calculated by counting the number of individual observations from the original tagging datasets from the relevant months (July-October or November-June).
(DOCX)

S4 Table. Mean sea surface temperatures predicted by an ensemble of three models (Institut Pierre Simon Laplace CMA5A-MR, the Geophysical Fluid Dynamics Laboratory ESM2M, and the Hadley Center Had-GEM2-ES) for each National Marine Sanctuary in the historical period (1980–2009) and the future period (2070–2099).
(DOCX)

S1 Fig. Predicted change in marine cold-spells in the California Current System from the historical period (1985–2014) to the future period (2070–2099) for three climate models. A, D, G, and J display predictions from the Hadley Center HadGEM2-ES. B, E, H, and K display predictions from the Institut Pierre Simon Laplace CM5A-MR and C, F, I, and L display yearly marine cold-spells predicted from the Geophysical Fluid Dynamics Laboratory ESM2M.
(TIF)

S2 Fig. Standard deviation of predicted percent change in core habitat between distinct MCS events for blue whales and leatherbacks in NMSs. Standard deviations of percent changes in core habitat are calculated between habitat responses to individual MCS events.
(TIF)

S3 Fig. Predicted historic habitat suitability and observed satellite tagging tracks for leatherback sea turtles and blue whales in the California Current System. Satellite tagging tracks are those used to construct the leatherback sea turtle and blue whale species distribution models published in Lezama-Ochoa et al. (2021) and Abrahms et al. (2019), respectively. Predicted habitat suitability values originate from the same species distribution models and have been averaged for the period 1980–2009.
(TIF)

Acknowledgments

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