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Divergent responses of highly migratory species to climate change in the California Current

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Abstract

Aim: Marine biodiversity faces unprecedented threats from anthropogenic climate change. Ecosystem responses to climate change have exhibited substantial variability in the direction and magnitude of redistribution, posing challenges for developing effective climate-adaptive marine management strategies.

Location: The California Current Ecosystem (CCE), USA.

Methods: We project suitable habitat for 10 highly migratory species in the California Current System using an ensemble of three high-resolution (~10 km) downscaled ocean projections under the Representative Concentration Pathway 8.5 (RCP8.5). Spanning the period from 1980 to 2100, our analysis focuses on assessing the direction and distance of distributional shifts, as well as changes in core habitat area for each species.

Results: Our findings reveal a divergent response among species to climate impacts. Specifically, four species were projected to undergo significant poleward shifts exceeding 100 km, and gain habitat (~7%–60%) in response to climate change. Conversely, six

species were projected to shift towards the coast, resulting in a loss of habitat ranging from 10% to 66% by the end of the century. These divergent responses could typically be characterized by the mode of thermoregulation (i.e. ectotherm vs. endotherm) and species' affiliations with cool and productive upwelled waters that are characteristic of the region. Furthermore, our study highlights an increase in niche overlap between protected species and those targeted by fisheries, which may lead to increased human interaction events under climate change.

Main Conclusions: By providing valuable species distribution projections, our research contributes to the understanding of climate change effects on marine biodiversity and offers critical insight and support for developing climate-ready management of protected and fished species.

1 | INTRODUCTION

Climate change is predicted to trigger significant changes in ocean circulation and environmental conditions, making it a pressing threat to marine species (Cheung et al., 2009). The Intergovernmental Panel on Climate Change (IPPC, 2007; Rosenzweig et al., 2008) projects a global range of sea surface temperature (SST) increases of 1–6°C by 2100, with significant impacts across all marine ecosystems (Doney et al., 2012). These impacts will likely include shifts in the distributions of many marine species (Cheung et al., 2015; Hazen et al., 2013) and are expected to happen faster than in the past (Pecl et al., 2017), particularly for populations whose ranges are not tied to physiographical features (Grose et al., 2020). In addition, eastern boundary upwelling systems are expected to experience changes in the intensity and timing of coastal upwelling, with uncertain implications for system phenology productivity (Bakun et al., 2015; Bograd et al., 2023).

In response to ongoing climate change, species may shift their range in search of more favourable habitats, disappearing locally or in some cases, globally from their current ranges (Albers et al., 2023; Grose et al., 2020; Polovina et al., 2011). Their capacity to survive will depend on their ability to adjust their ranges in accordance with new biophysical conditions and to adapt to new trophic interactions generated by varying environmental tolerances across predators and prey (Hazen et al., 2013; Pecl et al., 2017; Smith, Muhling, et al., 2021). These responses can vary significantly among species and therefore can present significant challenges and risks to the human communities and economies that depend on marine resources (Grose et al., 2020; Melbourne-Thomas et al., 2021; Mills et al., 2013; Pecl et al., 2014; Pinsky et al., 2019). For example, changing distributions of vulnerable species are expected to affect the efficacy of management strategies, such as marine protected areas, if the distribution or timing of

species' migrations shift in response to changing ocean conditions (Smith, Tommasi, et al., 2021). At the same time, changes in the location of target species or in the timing of fishing seasons may have important economic implications for local coastal communities and conservation concerns for future bycatch mitigation (Peer & Miller, 2014).

The California Current System (CCS) is a highly productive and biodiverse upwelling system that supports valuable fishery resources and protected species along the North American West Coast (Checkley Jr & Barth, 2009). Highly migratory species (HMS) (species that travel long distances and often cross domestic and international boundaries, e.g. whales, some shark species, billfishes and sea turtles) may be significantly impacted by climate change in CCS waters, especially during their foraging or breeding seasons (Hazen et al., 2013). These similar impacts have been also observed in terrestrial and aerial migratory species across seasonal or life-cycle scales (Albers et al., 2023). Projections of climate change in the CCS include changes in water column structure and biogeochemical properties, in addition to changes in upwelling intensity and timing (Pozo Buil et al., 2021). These environmental changes may trigger associated changes in phenology and distribution of some marine species in this ecosystem, including HMS and their prey (Hazen et al., 2013; Morley et al., 2018).

Species distribution models (SDMs) are commonly used as tools to explore relationships between species occurrences, abundance or behaviour and environmental variables (Elith & Leathwick, 2009). Ecological datasets to build SDMs for marine species can come from a variety of sources, including fisheries data, tracking data, fisheries-independent surveys or opportunistic sightings (Abrahms et al., 2019; Becker et al., 2020; Cañadas et al., 2018; Eguchi et al., 2017; Hazen et al., 2013). These datasets provide a rich source of information for implementing appropriate

management and conservation strategies under current, past or future environmental conditions (Free et al., 2020; Hazen et al., 2018). A number of SDMs have been applied to predict target, bycatch and protected marine species distributions in the CCS (Smith et al., 2023). There is an increasing need to understand the impacts and consequences of HMS responses to changing conditions in the CCS at a regional scale. The benefit of using downscaled regional models is that they allow for representation of important and specific regional-scale features usually missing or poorly represented when using coarse-resolution models (Pozo Buil et al., 2021). In addition, the use of multiple climate models can allow estimation of uncertainty (Brodie et al., 2022; Hazen et al., 2013).

Here, we present the projected distributions of 10 HMS in the CCS using SDMs applied to high-resolution (~10 km) downscaled ocean projections under the high emissions scenario representative concentration pathway (RCP8.5) across three climate models. This work represents a substantial advance from previous studies for the most economically and ecologically important HMS in the CCS. We describe the direction and distance of distributional shifts and changes in core habitat area for each species under each downscaled model. We investigate the consequences of species distributional shifts based on their importance for fisheries (as target species or bycatch) and for conservation (protected and vulnerable species). Projecting future HMS distributions provides an important step to help stakeholders anticipate and prioritize species of concern and account for conservation and management strategies that incorporate likely future conditions (Holsman et al., 2020).

2 | METHODS

2.1 | Species data

Ten HMS were selected for projecting future distributions based on data availability, their use of the CCS as a foraging hotspot, and economic and conservation importance for the CCS ecosystem (e.g. as catch and bycatch): blue shark (*Prionace glauca*), swordfish (*Xiphias gladius*), thresher shark (*Alopias vulpinus*), shortfin mako shark (*Isurus oxyrinchus*), leatherback sea turtle (*Dermochelys coriacea*), California sea lion (*Zalophus californianus*), humpback whale (*Megaptera novaeangliae*), fin whale (*Balaenoptera physalus*), northern right-dolphin whale (*Lissodelphis borealis*) and Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) (see Appendix S1).

2.2 | Historical modelling

SDMs for the 10 HMS (Becker et al., 2020; Brodie et al., 2018; Welch et al., 2019) were previously fitted using boosted regression trees (BRTs) models with physical environmental variables. These variables were extracted from an implementation of the regional ocean modelling system (ROMS) for the California Current region (Neveu et al., 2016) using historical re-analysis (1980–2010) and a near real-time product (2011–2020; oceanmodeling.ucsc.edu) (Table 1). The ROMS domain covers the region 30–48°N and 115.5–134°W (midway down Baja California to just south of Cape Flattery, WA) with 0.1° (~10 km) horizontal resolution and 42 terrain-following vertical levels (Veneziani et al., 2009). The SDMs were binomial, predicting the presence or absence of each species.

TABLE 1 Physical environmental variables.

Code	Variable name	Unit	Spatial resolution	Temporal resolution
sst	Sea surface temperature	°C	0.1°	Daily
sst_sd	Sea surface temperature st. dev	°C	0.3°	Daily
ssh	Sea surface height	m	0.1°	Daily
ssh_sd	Sea surface height st. dev.	m	0.3°	Daily
su	Surface eastward current velocity	m/s	0.1°	Daily
sustr	Surface eastward wind stress	N/m^2	0.1°	Daily
sv	Surface northward current velocity	m/s	0.1°	Daily
svstr	Surface northward wind stress	N/m^2	0.1°	Daily
curl	Wind stress curl	N/m^3	0.1°	Daily
eke	Eddy kinetic energy	m^2/s^2	0.1°	Daily
ild	Isothermal layer depth	m	0.1°	Daily
bv	Bulk buoyancy frequency	1/s	0.1°	Daily
lunar	Lunar illumination	%	0.1°	Daily
z	Bathymetry	m	0.1°	NA
z_sd	Bathymetry st. dev.	m	0.3°	NA

Note: These variables were extracted from an implementation of the Regional Ocean Modeling System (ROMS) for the California Current region (Neveu et al., 2016).

Abbreviation: sd, spatial standard deviation.

SDMs were fitted using different data types for each species (Appendix S1). 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 and leatherback turtle were obtained from satellite-linked tracking data collected during the Tagging of Pacific Predators program (2001–2009) (Block et al., 2011). Finally, data for whales and dolphins were obtained from surveys between 1991 and 2014 using systematic line-transect methods.

2.3 | Regional downscaled ocean projections

To force the HMS projections, we use daily output from three downscaled ocean projections for the CCS. These downscaled projections are based on an implementation of the same 0.1° ROMS domain described above, with bias-corrected forcing obtained from three earth system models (ESMs) for the period from 1980 to 2100 under the RCP8.5 climate scenario (Pozo Buil et al., 2021). Downscaled ESMs were selected to span the range of plausible futures for the CCS, and belong to the phase 5 of the coupled model intercomparison project (CMIP5) archive: the geophysical fluid dynamics laboratory (GFDL) ESM2M, Institut Pierre Simon Laplace (IPSL) CM5A-MR and the Hadley Center HadGEM2-ES (HAD). Because the magnitude of warming and other physical changes differed between ESMs, SDMs were projected using all three models to capture potential uncertainty and variability in physical conditions across models (Burgess et al., 2023). Data are available at https://oceanview.pfeg.noaa.gov/erddap/search/index.html?searchFor=ccs+roms.

The same suite of physical variables used for SDM training were obtained from regional ocean projections (at 0.1° resolution) (Pozo Buil et al., 2021) and used to force daily future HMS distributions (Table 1), with the exception of sea surface height (ssh). Sea surface height was excluded from the projections because the dynamics controlling projected sea level changes are different from those controlling ssh variability in the historical period. For example, while past ssh variability can be a proxy for ecologically important changes in ocean circulation, future ssh trends will be influenced by representing other processes (e.g. thermosteric sea level rise) that do not have the same ecological implications.

2.4 | Core habitat metrics

Daily projections of habitat suitability by species for each downscaled ESMs (GFDL, HAD, IPSL) were obtained for the period 1980–2100. The daily timesteps used to create the projections allowed for the quantification of change in species distribution through time (Champion et al., 2021). Core habitat was calculated to represent the most important habitat by species. It was calculated as the top 25% threshold quantile of projected habitat suitabilities over the first 30 years of the historical projected period (1985–2015) across

all days and averaged for each species and ESM (Hazen et al., 2013). Thresholds were used to exclude low values of habitat suitability (Appendix S3). The projected daily habitat suitabilities were reclassified into binary presences (1) and absences (0) based on the threshold values by species and ESM to obtain core habitat. To assess changes in suitable habitat, we calculated two metrics derived from core habitat:

- The centre of gravity in x (longitudes or eastings) and y (latitudes or northings) mean dimensions with their corresponding standard deviation was derived from the core habitat with the 'COGravity' function in the *SDMTools* package for R (Jeremy VanDerWal et al., 2014). The centre of gravity is calculated as the centre of mass of a species given by the latitude and longitude position, weighted by habitat suitability.
- The core habitat area was the size of the core habitat (in km^2) for a given species in a defined region. The core habitat area (in km^2) was derived from the core habitat and calculated using the 'ClassStat' function in *SDMTools* as the sum of suitable habitat in pixels considered core habitat.

2.5 | Changes in core habitat

Centre of gravity and core habitat area were calculated from average habitat suitabilities for the historical (1985–2015) and future (2070–2100) projected period. We calculated distributional shifts and percent change in core habitat area for each species for the future period relative to the historical period (Appendix S4). Distribution shifts were calculated as the future centre of gravity minus the historical centre of gravity, and described by direction (in degrees) and distance (in km). Direction and distance values were calculated for each species and averaged by ESM using the 'distGeo' and 'bearing' function, respectively, from the *geosphere* R package (Hijmans et al., 2012). The average direction across ESMs for each species was calculated using the 'average_bearing' function from the *hutils* R Package (Parsonage, 2022). Percent change in core habitat area was calculated as the future minus the historical period, divided by the historical period (Appendix S4). Additionally, the latitudinal distributional daily anomaly in the north–south dimension was calculated by subtracting the average centre of gravity across species (1980–2100) from each day in the projected period for each ESM and averaged by year (Appendix S4). This metric was used to describe temporal shifts in the north–south dimension of each species using time series plots for the years 1980 to 2100.

2.6 | Niche overlap for target versus protected species

The degree of overlap between the projections of species targeted by commercial fisheries and protected species in the CCS was calculated using the Schoener's D niche comparison metric for the period

1980–2100 and averaged across ESMs. Schoener (1968) D statistic for niche overlap varies between 0 (no overlap) and 1 (identical niches) (Carroll et al., 2019). For this comparison, we considered the target species swordfish, shortfin mako shark and thresher shark. California sea lion, leatherback turtle, humpback whale, fin whale, northern right-whale dolphin and Pacific white-sided dolphin were considered as protected species. Additionally, we calculated the degree of overlap between the projection of each target species separately versus each protected species. We calculated the Schoener index as described in Warren et al. (2008) using the 'raster.overlap' function from the *ENMTools* package (Warren et al., 2021).
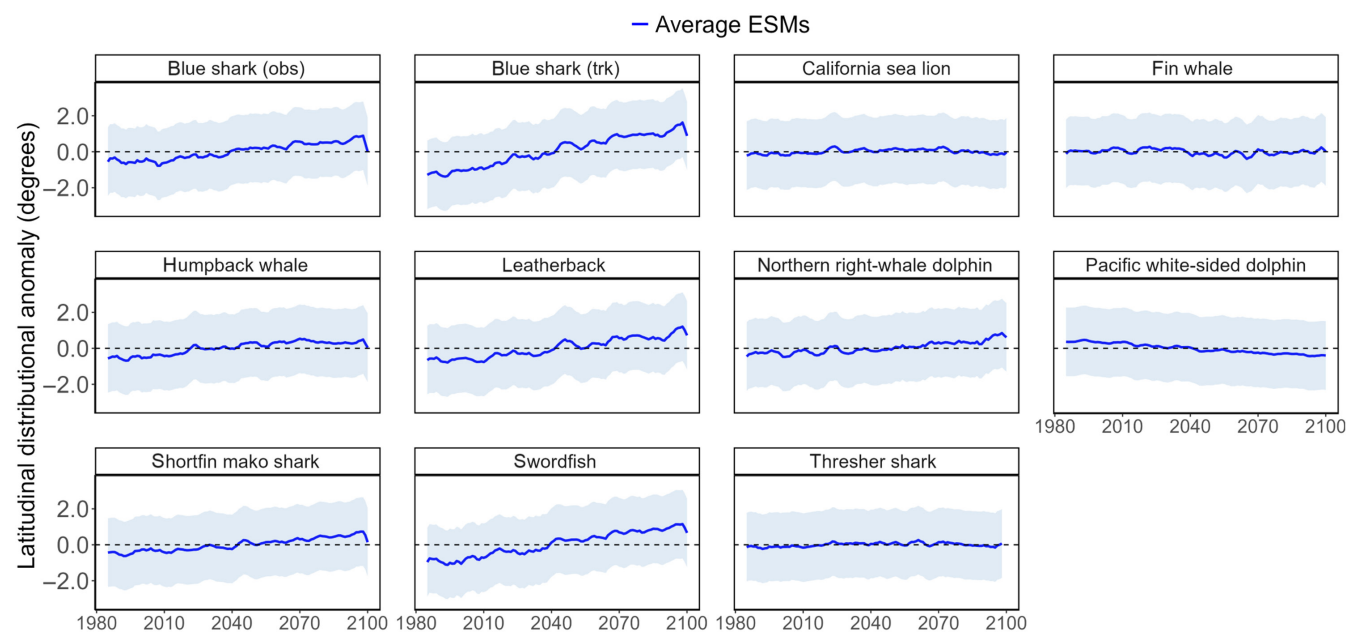
3 | RESULTS

3.1 | Changes in core habitat

Projections in the CCS indicated variable responses to climate change among species. We identified two patterns based on the distributional shifts: (i) blue shark, swordfish, shortfin mako shark and leatherback turtle are expected to shift poleward and offshore due to increased habitat suitability in northern waters, while (ii) thresher shark, California sea lion and whales and dolphins are expected to shift southward and/or constrain their habitat towards the coast; with the exception of the northern right-whale dolphin shifting north (Figures 1, 2 and Appendix S5). Specifically, California sea lion, thresher shark and fin whale did not show important shifts. These distributional shifts were mirrored by expected changes in projected habitat suitability (Appendix S6). Blue shark, swordfish,

shortfin mako shark and leatherback turtle are expected to gain suitable habitat, and thresher shark and the marine mammals (humpback whale, northern right-whale dolphin and Pacific white-sided dolphin, California sea lion) are projected to lose suitable habitat in the CCS (Figure 2 and Appendix S5). For blue sharks, when comparing models based on observer versus tracking data, there were no considerable differences in projected distributional shifts although more interannual variability between ESMs was apparent in the tracking data (Figure 1 and Appendix S5). The relative importance of each physical variable in explaining the historical distribution of the HMS varied among species, with bathymetry and sea surface temperature ranked as the top variables across all species (Appendix S2).

Comparing species that moved north to those that moved south, there was variation in both the direction and magnitude of movements (Table 2, Appendix S6). The species expected to move poleward generally have shifts of more than 100 km and in a direction of ~300° (NW) from their current centre of gravity. In contrast, species expected to move southward shifted less than 100 km. Species with smallest displacements (thresher sharks, California sea lion and humpback whale) shifted towards the coast in the NE direction (Table 2, Appendix S6). Swordfish, blue shark and leatherback turtles are expected to experience the largest poleward range expansions. For example, swordfish are expected to shift an average of 198 km at a bearing of 339° between the historical and future periods, with no variations among model projections (Table 2, Appendix S6). Their projected habitat is expected to concomitantly decrease along the California coast and to expand poleward and offshore (Appendix S6). In contrast, thresher shark and fin whales experienced the lowest shift across ESMs, with averages of 33 and 23 km respectively

FIGURE 1 Time series of the projected change in the latitudinal distributional anomaly (in degrees). Results are shown for the average of the 3 ESMs (dark blue line) and their corresponding spread (standard deviation shaded in light blue). The latitudinal distributional anomaly was calculated by subtracting the average centre of gravity given by north–south dimension across species (1980–2100) from each day in the projected period. Species ordered alphabetically. obs, observer data; trk, tracking data.
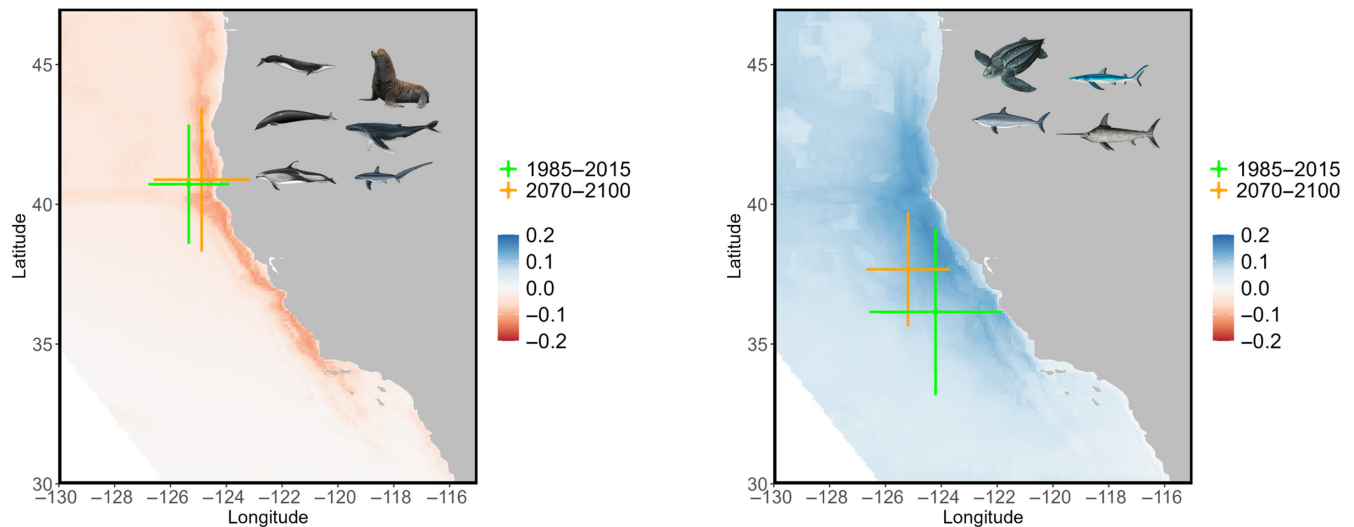
FIGURE 2 Differences (future minus historical) in projected habitat suitabilities for species which are expected to lose (left panel) core habitat area ('habitat loss': marine mammals and thresher shark) and species which are expected to gain (right panel) core habitat area ('habitat gain': blue shark, leatherback turtle, mako shark and swordfish) averaged by ESMs. Red represents predicted loss in habitat suitability and blue gain in habitat suitability. Centre of gravity and their corresponding 1± standard deviation calculated across species and ESM are represented for the historical (green crosses) and future (orange crosses) periods.

TABLE 2 Distance (in km), direction (in degrees; with northward representing 0° and 360°, eastward 90°, southward 180° and westward 270°) of shift and core habitat area change (%) with the corresponding standard deviation and standard error by species averaged by the three ESMs between the future period (2070–2100) minus the historical projected period (1985–2015).

Species	Distance (km)	SD (km)	Direction (degrees)	SD (degrees)	Percent change core habitat area (%)	SE (habitat)
Northern right whale dolphin	72	40	123 (SE)	201	−66	4
California sea lion	86	22	75 (NE)	31	−66	8
Humpback whale	114	19	31 (NE)	17	−60	9
Thresher shark	33	22	63 (NE)	64	−32	4
Pacific white-sided dolphin	95	22	143 (SE)	1	−14	2
Fin whale	23	11	258 (SW)	85	−10	4
Blue shark (trk)	267	77	332 (NW)	2	7	4
Blue shark (obs)	126	15	343 (NW)	2	43	3
Swordfish	198	34	339 (NW)	1	52	5
Leatherback turtle	204	60	317 (NW)	16	57	17
Shortfin mako shark	101	22	14.8 (NE)	2	62	13

*Note*: Negative habitat change values represent loss of habitat.

Abbreviations: NE, north-east; obs, observer data; SE, south-east; SW, south-west; trk, tracking data.

(Table 2, Appendix S6). Projected habitat suitability for thresher sharks is expected to decrease offshore and be more constrained to the coast (Appendix S6), with no significant shift. Species changes are available in Appendices S7–S17. Comparing the observer and tracking data for the blue shark tracking data resulted in greater shifts (average of 267 km) compared to the observer data (average of 126 km) across ESMs (Table 2).

We quantified changes in the core habitat area (in km²) between the historical (1985–2015) and future periods (1970–2100). Interspecific comparisons reveal the potential for both core habitat loss and gain within the CCS under climate change (Figure 3;

Table 2). Northern right whale dolphins and California sea lions had more than 66% loss in core habitat area, followed by humpback whales (60%). In contrast, most of the species shifting poleward and offshore are projected to gain habitat with an overall increase in core habitat area for the leatherback turtle (>50%), swordfish (>50%) and blue shark (observer data, >40%). All species showed changes in core habitat area across years. In general, those species projected to expand their habitat are expected to be more resilient to future environmental changes than those limited to coastal or local areas with more restricted or specific seasonal environment preferences.

Core habitat area change (1985–2015) vs. (2070–2100)

average ■ Gain ■ Loss
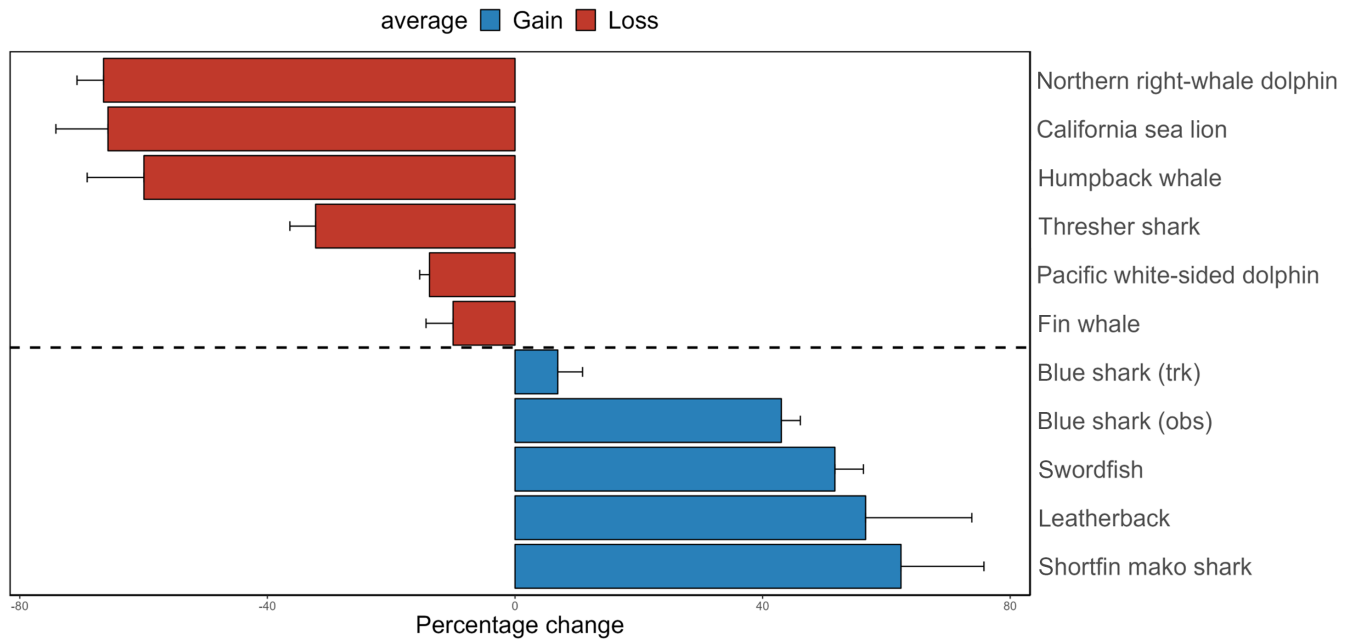
FIGURE 3 Percent change (in %) of the difference in core habitat area (in km^2) averaged by the three ESMs (gain core habitat area in blue, loss core habitat area in red) calculated as the future projected period (2070–2100) minus the historical period (1985–2015), divided by the historical period. Error bars represent one standard error calculated across species. obs, observer data; trk, tracking data.

FIGURE 4 Time series of the niche overlap using the Schoener's D index averaged across ESMs (dark blue line) and their corresponding spread (standard deviation shaded in light blue) and between target (swordfish, shortfin mako shark and thresher shark; silhouettes in black) versus protected species (California sea lion, leatherback turtle, humpback whale, fin whale, northern right-whale dolphin and Pacific white-sided dolphin; silhouettes in blue).
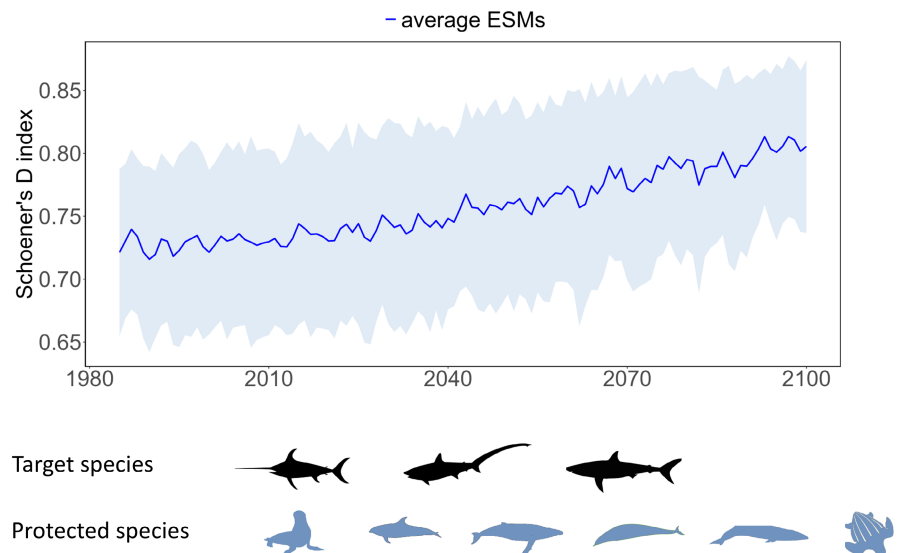
3.2 | Niche overlap for target versus protected species

Schoener's index showed a 5%–10% increase in niche overlap between target and protected species by the period 2070–2100. This increased overlap may intensify spatial interactions between target and protected species, as a result of an expansion of target species habitat into areas inhabited by protected species (Figure 4). This trend is particularly notable for swordfish and shortfin mako shark, with both species projected to expand their current habitat and expected to increase their niche overlap with leatherback turtle (5%), humpback whale (10%), northern right-whale dolphin

(20%) and Pacific white-sided dolphin (5%) (Appendix S18). In contrast, their niche overlap is expected to decrease with California sea lions (20%) and fin whales (10%). Finally, in the case of the thresher shark, niche overlap with protected species is expected to decrease (Appendix S18).

4 | DISCUSSION

Climate change is impacting marine systems and the species that inhabit them, causing distribution shifts as mobile species follow preferred habitats. Projections of future habitat change and

distribution shifts are important for anticipating climate change impacts in marine systems and developing adaptation strategies (Doney et al., 2012; Pecl et al., 2017; Poloczanska et al., 2016). Here, we projected the distributions of 10 HMS within the CCS. These species have different ecological characteristics, anthropogenic pressures and thermal and diet preferences, giving us the opportunity to identify patterns in distribution shifts across taxa. We found that by the end of the 21st century, climate change is likely to cause shifts in the location and amount of core habitat for the majority of these HMS. We demonstrate the utility of using SDMs and climate models for identifying HMS species that are most at risk of habitat loss and to inform climate-ready management strategies to sustainably manage these species in the century to come.

4.1 | Distributional shifts of HMS in response to changing conditions

In response to climate change, species may shift poleward in search of more favourable thermal or prey conditions (Melbourne-Thomas et al., 2021). Distribution shifts are one of the most commonly reported responses to marine climate change and have been observed for marine species across all ocean regions (Poloczanska et al., 2013, 2016). Our results show that half of the HMS species we examined are projected to shift their distribution poleward, agreeing with observations in the last few decades and short-term patterns linked to warming events like the marine heatwave and El Nino events (Cheung et al., 2009; Jones & Cheung, 2015; Palacios-Abrantes et al., 2023; Perry et al., 2005; Poloczanska et al., 2013). Furthermore, our analyses show variability in the directionality and magnitude of species distributions shifts in response to climate change in the CCS. Species projected to expand their habitat may be more resilient to future environmental changes than those limited to coastal or local areas with more restricted or specific seasonal environment preferences (Appendix S6). Species projected to shift northward and offshore (swordfish, blue shark, mako shark and leatherback turtle) also have major increases in suitable habitat (Figure 2; Table 2). These species have broad thermal tolerances and occupy diverse habitats (i.e. from surface to deep waters, and from the tropics and temperate regions) (Block et al., 2011; Brodie et al., 2018), possibly providing higher adaptive capacity to novel conditions in the CCS.

Previous studies in the eastern North Pacific predicted changes in core habitat for some top predator species, including leatherback turtles, California sea lion, shortfin mako shark and blue shark (Hazen et al., 2013). Our study found similar results in the case of projected gain of habitat for leatherback sea turtles and loss of habitat for California sea lions (Figure 3; Table 2). In contrast, blue shark and mako shark were predicted to lose habitat by Hazen et al. (2013) while here we found a gain of habitat for the same species. The main reasons for the differences found in this study compared with Hazen et al., 2013 are likely the different scale of

projections, SDMs applied and environmental variables included in the models. While Hazen et al. (2013) used CMIP3 projections at coarse resolution, we used three dynamically downscaled CMIP5 projections, with the benefit of capturing the impact (e.g. changes in coastal upwelling) at local scales and accounting for uncertainty. Hazen et al. used Generalized Additive Models (GAMs), while we used BRTs, with differences between models when extrapolated (Becker et al., 2020; Brodie et al., 2022). Finally, we did not include chlorophyll or biogeochemical predictors. Instead, we used other physical predictors which were important for predicting species distributions (Appendix S2). It is not very common for these projection studies to be updated or revisited, and the differences between the two studies here could suggest that many of the choices we make when combining models to project future distributions can be very important. Comparing the projected distributions of other coastal pelagic species and their predators across different regions (i.e. US East Coast, Braun et al. (2023)) can offer more insight on the impacts that climate change may have on these HMS globally.

Species with narrow thermal tolerances or specific habitat requirements may have different intensity of climate change impacts (Jones & Cheung, 2015). Some species in this study were projected to lose part of their habitat, while showing smaller shifts in their distribution (Figure 2; Table 2). These species (California sea lion, thresher sharks, whales and dolphins) may have more limited thermal tolerances or their distributions may be more tied to geographical features. For example, thresher shark habitat is more restricted to waters inshore of the 1000 m isobath, and their preferred sea surface temperature range in the CCS is between 12 and 18°C (Brodie et al., 2018). Projections showed a loss of habitat for this species towards the coast. California sea lions are central-place foragers whose distribution is tied to suitable pupping and haul-out sites (Costa & Valenzuela-Toro, 2021). As a result, they are limited in the extent to which they can move latitudinally or offshore to avoid unfavourable ocean conditions. Those areas showing loss of habitat may be described as areas at high risk of climate change impacts.

4.2 | Ecological implications of HMS distribution shifts

Shifts in HMS distributions can have ecological consequences; for example, how these species experience mismatches between predator and prey distributions and changes in species phenology (Morley et al., 2018; Poloczanska et al., 2013). Recent studies on forage species [e.g. anchovy (*Engraulis mordax*), rockfishes (*Sebastes* spp.), sardine (*Sardinops sagax*) and market squid (*Doryteuthis opalescens*)] in the CCS suggest that many are likely to move northward as a result of warming temperature, potentially impacting their predators and the fisheries they support (Chasco et al., 2022; Muhling et al., 2020; Smith, Muhling, et al., 2021). Predator and prey shifts may occur at different distances and

directions, impacting specialized predators as food availability is reduced, compared to prey-switching generalist predators (Hazen et al., 2013). Potential phenological changes driven by climate change include shifts in the time or frequency of reproduction, foraging or migration, depending on whether the cues used for these processes are responsive to environmental variability. Some of the species included in this study migrate between the CCS and the offshore North Pacific as part of their life cycles (e.g. swordfish, blue shark and shortfin mako shark (Nasby-Lucas et al., 2019)). Shifts in suitable habitat for these species may impact their migration routes, the timing of their presence in the CCS, and their exposure to anthropogenic impacts.

For example, leatherback turtle habitat is projected to move north and offshore, and expand off Oregon and Washington (Figure 1; Table 2, Appendices S6 and S13). Waters off central California are currently a critical foraging area for leatherback turtles, where they feed in areas where the coastline physiography leads to dense aggregations of their jellyfish prey (Benson et al., 2011). Those areas retained their importance in future projections, however, leatherback populations could still face population pressure or a decrease in reproductive output (Saba et al., 2007) if their main prey in coastal areas becomes less abundant or also experiences distribution shifts. Anthropogenic impacts on nesting beach habitat in the western Pacific, and fishery bycatch in international high seas waters, place additional pressure on leatherbacks and illustrate the complexity of managing these highly migratory and multiple habitat dependent species (Benson et al., 2011). Future projections could consider multiple ecological habitats (e.g. nesting, foraging and migration) separately as well as include biogeochemical variables (e.g. chlorophyll-*a*, oxygen and primary productivity) or prey information to help account for differences in area occupied and predator–prey relationships. Future work would benefit from specific consideration of the prey base in projections.

Projections of future habitat for whales and temperate dolphins in this study show overall habitat loss in response to environmental conditions in agreement with previous work (MacLeod, 2009; Pecl et al., 2017; Pinsky et al., 2021). For example, projections suggest a constraint of habitat along the California coast and a shift poleward of 100 km for humpback whales (Appendices S6 and S14). Humpback whales visit feeding grounds in California waters during April–November annually. If shifting habitat suitability results in changes to the timing of this migration, it could lead to a mismatch between breeding and feeding seasons, with negative consequences for reproductive success.

4.3 | Additional considerations: Strengths, limitations and future refinements of our projections

This study integrates a unique, large, diverse and long-term dataset, from which SDMs were built for diverse taxa with different ecological characteristics and vulnerabilities. The use

of consistent methodologies applied across SDMs (i.e. using BRTs with similar parametrization when fitted) allowed us to make comparisons among species. The availability of SDMs coming from different data sources (e.g. blue shark) allows us to describe similarities and differences in core habitat use of the species and identify the best source to be applied for future projections. For example, blue shark projections showed differences by data type, whereas projections using fishery-dependent data show an associated bias coming from fishing behaviour. This is consistent with other studies that have identified the role of sampling bias in projections (Braun et al., 2023; Karp et al., 2019), and we show that using multiple datasets strengthens our results and allows us to identify possible bias. Our use of multiple downscaled earth system models was able to more finely resolve the spatial dynamics of species distribution projections, while simultaneously allowing us to estimate uncertainty.

Species distribution projections encompass uncertainty associated with the scenario or climate model used and the parameters and species distribution model integrated (Brodie et al., 2022; Morley et al., 2018). We used three downscaled ESMs (GFDL, HAD, IPSL) under one climate change scenario (RCP8.5) to encompass such uncertainty but there are potential areas for expansion to strengthen the analysis, such as including additional climate models, multiple scenarios and multiple species distribution models and other ecological models (Karp et al., 2019; Pecl et al., 2017; Smith et al., 2023). The future use of the CMIP6 model for modelling species distributions is also highly recommended. Gaining access to consistent, high-quality environmental and species distribution data for validating and improving historical species distributions is necessary to improve future projections (Pecl et al., 2017).

The SDMs in this analysis are correlative (identifying correlative relationships between species occurrence and habitat covariates), and the model projections assume (i) that important species-specific covariates are correctly identified, especially when the covariates themselves are correlated, and (ii) that the correlations will persist through time. If, for example, a SDM gives SST greater importance than bathymetry (these are somewhat correlated in the CCS), while the species is clearly linked to bathymetric features, then the projections could be inaccurate. The cetacean models were derived in Becker et al. (2020), who noted that the BRT models did not perform as well as other modelling frameworks when making novel predictions. This underscores the need to further explore other models, to assess accuracy and uncertainty in model predictions. For example, comparisons between models including a different set of environmental variables and spatial components as well as comparisons between response variables (e.g. density and presence-absence), and model type (e.g. GAMs and BRTs) will improve our understanding of the weaknesses and strengths of these projections. Due to the convex curvature of the US west coast, centroids for some species were located on land. While a centroid is coarse and does not necessarily represent where species actually are, it still captures the relative relocations of preferred habitat among species. The exclusion of sea

surface height during the projections may have had an impact on some of the marine mammals projections. For example, fin whales did not show any significant detectable shift, even though there are past distribution changes associated with regime shifts (Rice et al., 2015). Similarly, northern right whale dolphins and Pacific white-sided dolphins have very similar habitats (slope waters, extending offshore and across the Pacific north of about 45° N) and often co-occur in mixed schools, but the models projected different trends. Future models should address and account for differences in habitat shifts depending on the covariates selected.

Our analysis uses habitat suitability as the metric of change, but it is important to recognize that the amount of suitable habitat does not directly inform the number of animals present. For management, the actual number of animals is often more important, as a reduction in suitable habitat could mean there is less spatial overlap with human activities such as fishing (less risk of interaction), or it could conversely mean that the animals are compressed into a smaller area, increasing densities and /or changes in nature of the species/ habitat relationships, which would tend to increase the risk of interactions. Such patterns have been described for humpback whales and fishery entanglements and for northern right whale density and distribution patterns during the marine heat wave of 2014 (Becker et al., 2018; Santora et al., 2020). Models that can take into account changes in the actual number or density of HMS species will be useful for management.

Seasonality in distribution is quite pronounced for some species (and for some fisheries), and our use of annual average values for the projections limits our interpretation to the mean annual patterns. However, the mean could remain unchanged at the same time that seasonal patterns become more or less variable. If impacts on species are seasonal, then a finer temporal scale may be warranted in future projection studies (Braun et al., 2023). Similarly, it would be interesting to compare metrics across North Pacific versus CCS to detect possible bias associated with the smaller study domain. Additionally, the identification of hotspots, critical habitat and corridors should be considered through the development of connectivity analysis that helps to design conservation measures again threats usually occurring through the geographical ranges of the species (Kot et al., 2023).

4.4 | Implications of HMS shifts for management and conservation

Climate change is expected to impact species distributions, altering the locations of profitable fishing grounds, fisheries impacts on protected species and ecosystem services (Grose et al., 2020; Pinsky et al., 2021). While some of these species' shifts are expected to trigger economic losses, others are likely to create new fishing opportunities for local communities (Kleisner et al., 2017; Smith et al., 2023). Both of these potential future scenarios may increase fishing conflicts via distribution of new quotas and allocation rights (Hazen et al., 2013; Karp et al., 2019). Projected climate-driven

shifts can redistribute species across national and international boundaries, exacerbating existing or creating political conflicts between regions with economic consequences (Melbourne-Thomas et al., 2021; Morley et al., 2018; Pecl et al., 2017; Pinsky et al., 2019; Schroeder et al., 2022). Projections of species shifts across transboundary zones (Blair et al., 2022) can be utilized for proactive approaches to identify species most at risk and areas to prioritize for management intervention. These models can be combined with fishery and economic models (Kaplan et al., 2012) to prevent future species losses or declines in focal areas.

In the CCS, an increase and offshore shift in habitat for managed species (Table 2, Appendix S6) may challenge conservation and management policies, as these are more easily implemented in national waters than on the high seas. At the same time, a target species shifting across borders (Pinsky et al., 2021) may expose them to new regulations and threats with direct geopolitical and economic implications (Melbourne-Thomas et al., 2021). For example, swordfish is an economically important species for fisheries in the CCS; thus, any shift in the distribution of swordfish (and, consequently, fishing effort) will be of concern for fishery stakeholders. Swordfish are targeted using different fishing gears in the US West Coast EEZ (drift gillnet, buoy gear and harpoon) than they are in the offshore North Pacific (pelagic longlines). A shift in swordfish distribution could therefore impact fishery-dependent indices of abundance that are input to the stock assessment, as well as the accessibility of the stock to fishing fleets from different countries.

Protected and endangered species (turtles, marine mammals) may not remain within the current boundaries of marine protected areas (MPAs) or seasonal closures if their distributions or migration routes shift, making these measures potentially ineffective. As such shifts occur in novel environments expected under climate change, protective measures for endangered species will need to be adapted (Melbourne-Thomas et al., 2021). The 2014–2016 northeast Pacific marine heatwave changed the abundance and distribution of humpback whale prey with a consequent shift of whales to the coast and with an increase in the number of whale entanglements in fishing gear (Santora et al., 2020). If the habitat off California becomes less suitable, this species could be exposed to new anthropogenic threats with negative consequences for their populations and it could have major consideration for species conservation and management. Additionally, Becker et al. (2018) showed that northern right whale habitat shrunk dramatically during the MHW of 2014, but the total number of animals was actually high. This suggests that animals were more concentrated in a smaller area with increasing densities and/or changes in nature of the species/habitat relationships, which would tend to increase the risk of interactions and with future direct implication for management.

As species are shifting geographically under climate change to follow suitable habitat conditions, planning management measures in advance is essential to protect the most vulnerable species (Bonebrake et al., 2018). Transition from static to dynamic spatial management may help to identify mismatches between future species distributions and spatial boundaries. New MPA boundaries could

consider projected species' ranges, or allow for flexibility through time using adaptive or dynamic management approaches for those species with large dynamic habitats (Conners et al., 2022; Hobday et al., 2018; Maxwell et al., 2020; Smith, Tommasi, et al., 2021). Identification of hotspots or climate refugia, where distributional changes are expected to be identified earlier (Hobday & Pecl, 2014), can be potential candidates for future protected areas (Bonebrake et al., 2018).

At the same time, National Marine Sanctuaries and proposed expansions of protected areas could potentially adapt to shifting habitat of marine mammals and turtles, and future studies could predict such changes relative to existing National Marine Sanctuaries boundaries and MPAs. The possible disruption of cultural connections to the iconic species is an important issue that requires special attention (Pecl et al., 2017). Distribution shifts of protected species may also impact ecosystem services (e.g. whale watching tourism, ship-strike risk and shipping) that could cascade into economic consequences for local communities. Distribution shifts and future niche overlap of both target and protected species (Figure 4; Appendix S18) also have the potential to increase bycatch or change the timing and location of bycatch hotspots, reducing the effectiveness of management measures (Karp et al., 2019). The increased overlap may intensify spatial interactions between target and protected species. Existing tools such as Ecocast is an example of how shifts in distribution for target species could impact bycatch measures (Hazen et al., 2018). This tool combined with dynamic versus static scenarios of area closures (Smith, Tommasi, et al., 2021) could be included in future management plans.

Climate-driven species shifts are already one of the most notable impacts of ocean warming at local and global scales (Melbourne-Thomas et al., 2021). Understanding future species shifts is necessary to minimize negative short- and long-term impacts. Both fisheries stakeholders and managers could be equipped with the best available scientific and management tools, such as indicators and thresholds, over a range of timescales to proactively plan for the protection of economically valuable and vulnerable species (Pecl et al., 2014). We recommend the development and integration of multi-species ecological indicators based on thresholds that are easy to understand and interpret for stakeholders, in order to inform decisions about environmental and species distributional changes in the CCS (Koehn et al., 2022). Examining changes with new environmental (e.g. Coastal Upwelling Transport Index, CUTI; Jacox et al. (2018)) and ecological indices (e.g. habitat compression; Schroeder et al., 2022) under different climate scenarios is needed to understand future shifts (Koehn et al., 2022; Schroeder et al., 2022). Collaboration, coordination and communication across stakeholder groups will be required to prepare for and achieve sustainable management for species shifts and to resolve future economic and jurisdictional conflicts.

CONFLICT OF INTEREST STATEMENT
The authors declare no competing interests.

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The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13800.

DATA AVAILABILITY STATEMENT
Monthly downscaled climate projections are available online (https://oceanview.pfeg.noaa.gov/erddap/search/index.html?searchFor=ccs+roms). Main outputs from the projections for each ESM and species are included in the supplementary material.

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BIOSKETCH

Nerea Lezama-Ochoa is a marine ecologist with broad interests in spatial and movement ecology, global change biology and conservation biology. The team of authors includes ecologists, oceanographers and modellers interested in impacts of climate change in oceanographical processes and animal ecology.

Author contributions: NLO, SB, HW, MC, SB and EH designated the study. NLO performed the analysis and wrote the first version of the manuscript. SB, HW, SB and EH provided code and guidance for the methods. SB, HW, MJ, BC, EB, SB, KF, CB, RB, SB and EH coordinated the work and provided technical guidance. All the authors contributed to the final version of the manuscript.

SUPPORTING INFORMATION

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