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Marine Heatwaves and Climate-Driven Warming Impact Availability of Sardine Subpopulations to Northeast Pacific Fishing Ports

Barbara A. Muhling[1,2] | Juan P. Zwolinski[1,2] | Peter T. Kuriyama[2] | Toby D. Auth[3] | Richard D. Brodeur[4] | Sylvia P. A. Jiménez Rosenberg[5] | Gerardo Aceves-Medina[5] | Jose Augusto Valencia Gasti[6] | Michael G. Jacox[1,7,8] | Mercedes Pozo Buil[1,7] | Jerome Fiechter[9] | Felipe J. Quezada Escalona[1,2,10] | Desiree Tommasi[1,2]

[1]Institute of Marine Sciences Fisheries Collaborative Program, University of California, Santa Cruz, California, USA | [2]Southwest Fisheries Science Center, National Oceanic and Atmospheric Administration, La Jolla, California, USA | [3]Pacific States Marine Fisheries Commission, Newport, Oregon, USA | [4]Northwest Fisheries Science Center National Oceanic and Atmospheric Administration, Newport, Oregon, USA | [5]Instituto Politécnico Nacional – Centro Interdisciplinario de Ciencias Marinas, La Paz, Baja California Sur, Mexico | [6]Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Ensenada, Mexico | [7]Southwest Fisheries Science Center, National Oceanic and Atmospheric Administration, Monterey, California, USA | [8]Physical Sciences Laboratory, National Oceanic and Atmospheric Administration, Boulder, Colorado, USA | [9]Ocean Sciences Department, University of California, Santa Cruz, California, USA | [10]Departamento de Economía, Universidad de Concepción, Concepción, Chile

Correspondence: Barbara A. Muhling (bmuhling@ucsc.edu)

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ABSTRACT

Changing ocean conditions are leading to spatial redistribution of many marine species, including those that support fisheries. A combination of gradual climate trends and shorter-lived extreme events, such as marine heatwaves, can change the availability of species or stocks to fishing ports, impacting fishing communities and challenging fisheries management frameworks. Pacific sardine (*Sardinops sagax*) in the California Current System are currently considered as two subpopulations for management purposes. They are separated from each other using oceanographic conditions, based on the assumption that each subpopulation is associated with different habitats and geographic areas. However, as climate change and marine heatwaves lead to increasingly novel environmental conditions in the region, habitat-based assignments may become impractical or unrealistic. In this study, we use generalized additive models to define sea surface temperature and surface chlorophyll conditions associated with the occurrence of multiple sardine life stages in fishery-independent surveys conducted in the California Current System. We then show how the spatial distribution of habitats across life stages and putative subpopulations may be influenced by both gradual climate change and marine heatwaves. Our results highlight the potential impacts of changing ocean conditions near major sardine landing ports. During recent marine heatwaves, habitat associated with the northern subpopulation became less available to southern California Current ports, and this trend is projected to continue through the end of the 21st century. Future spatial shifts in sardine habitat may increasingly challenge the practicality of habitat-based subpopulation separation and introduce more uncertainty into management frameworks.

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1 | Introduction

Climate change is well recognized as a driver of spatial distribution shifts in marine species, including managed stocks (Poloczanska et al. 2013; O'Leary et al. 2022). Against this background of directional warming, short-term thermal extremes such as "marine heatwaves" (Jacox 2019; Oliver et al. 2021) can cause rapid and substantial ecosystem effects, including range extensions or contractions (Cavole et al. 2016) and broader biological and socioeconomic impacts (Smith, Burrows, et al. 2021). This combination of gradual climate change and periodic anomalous conditions has been termed "press and pulse": where long-term trends and short-term extreme events can intersect to cause unprecedented impacts to both ecosystems and the human communities that rely on them (Harris et al. 2018).

Ongoing warming in the coming decades is likely to lead to further species distribution shifts, which may be exacerbated during extreme events such as marine heatwaves. Managed species or stocks may move across static management boundaries, changing their availability to different fishing fleets (Palacios-Abrantes et al. 2020; Franco et al. 2022). As a result, some fishing communities may face declines in economic opportunities unless they can adapt through catching new species or fishing in new locations (Rogers et al. 2019; Ojea et al. 2020). Fisheries management frameworks that have historically relied on certain stocks being available for exploitation within the waters of certain states or nations can also become less effective and less equitable (Vogel et al. 2023). To enable climate-ready fisheries management, there is thus a need to anticipate spatial distribution shifts that may challenge management processes (Karp et al. 2019).

The majority of wild-capture fisheries around the world are assessed and managed at the level of single-species stocks (Cadrin et al. 2023). In some cases, stocks may span multiple countries or jurisdictions. The fisheries management process can become political when delineation of stock boundaries impacts who has management authority over a stock and who is allowed to harvest it (Munro 1979; Cadrin et al. 2023). It is often difficult to determine the stock structure of a species, especially for highly mobile animals. Stocks have been defined using genetic characteristics, geographic variability in traits, distinct habitat associations, or management boundaries (Reiss et al. 2009; Neat et al. 2014; Secor 2014; Kerr et al. 2017). Stock separation can be easier when stocks show less mixing geographically. For example, Atlantic cod (*Gadus morhua*) around the British Isles have multiple distinct population units, each of which is associated with different habitat conditions (Heath et al. 2014; Neat et al. 2014). In contrast, the two stocks of Atlantic bluefin tuna (*Thunnus thynnus*) occupy distinct spawning areas, but juveniles and adults do not associate with particular environmental conditions and mix extensively on foraging grounds (Kerr et al. 2017; Díaz-Arce et al. 2023). Depending on the biology of species, climate-driven distribution shifts could therefore change not only the availability of species to place-based fishing fleets and fishing ports but also the availability of stocks within species.

Pacific sardine (*Sardinops sagax*) historically supported valuable fisheries in the California Current System (CCS). During the 1950s, the sardine population collapsed, likely driven by a combination of unfavorable environmental conditions and fishing pressure (McFarlane et al. 2002). While sardine recovered temporarily in the 1990s, their abundance began to decline again in the mid-2000s, and the fishery was closed in 2015. As well as supporting fisheries, sardine are important as prey for a wide variety of predators (Szoboszlai et al. 2015). Pacific sardine have been one of the most intensively studied species in the eastern North Pacific since the population crash and subsequent fisheries closures in the 1950s–1960s (Herrick et al. 2006; Checkley et al. 2017). Despite this scrutiny, key biological features of the species remain incompletely understood, including drivers of recruitment, response to warming conditions, and subpopulation structure (Thompson, Ben-Aderet, et al. 2022; Free et al. 2023).

Sardine are managed by the Pacific Fishery Management Council (Council) under the hypothesis that there are three separate subpopulations (i.e., reproductively isolated units: Marr 1960) off the North American west coast. The northern subpopulation is defined as being distributed from the state of Baja California, Mexico, to Vancouver Island, British Columbia, while the southern subpopulation is distributed from the southern Baja California peninsula to southern California (Yau 2023; Kuriyama et al. 2024). A third subpopulation is found primarily in the Gulf of California. Importantly, sardine from northern and southern subpopulations can migrate seasonally, especially when biomass is high, moving northwards in warmer months and southwards in cooler months. As a result, fish assumed to be from the southern subpopulation are present off southern California in warmer months, while fish assumed to be from the northern subpopulation are found in this area in cooler months (Zwolinski and Demer 2023). The geographic distributions of the two putative subpopulations are thus not completely separate.

Per the Council's Fishery Management Plan, only the northern subpopulation is managed (Kuriyama et al. 2024). To facilitate this approach, a habitat model was first created by Zwolinski et al. (2011) and then updated by Zwolinski and Demer (2023) to separate out northern subpopulation fisheries landings and fishery-independent survey biomass estimates before these are used to inform the stock assessment model. This habitat model was trained on occurrences of sardine eggs collected during spring from 1998 to 2019, between 30° N and 37° N, under the assumption that this generally covers the spawning area of northern subpopulation sardine (Zwolinski et al. 2011).

Although only the putative northern subpopulation of sardine is managed, previous studies of genetic characteristics have shown no distinction between the northern and southern subpopulations, at least over longer evolutionary timescales (see Adams 2023 and references therein). In addition, laboratory experiments show that their critical thermal limits and preferred temperature ranges are very similar (Martínez-Porchas et al. 2009; Pribyl et al. 2016). While habitat-based assignments have been employed to separate out northern subpopulation sardine for the past decade, it is unclear if they are separating biologically unique groups. Nevertheless, current management operates using this framework. The habitat-based assignments are important to current fisheries management practices, as the fishery for the northern subpopulation has been closed due to low biomass since 2015, despite the availability of putative southern subpopulation fish off southern California (Kuriyama et al. 2020; Stierhoff et al. 2020; Enciso-Enciso et al. 2023). In addition, the CCS has been impacted by several severe marine heatwaves in the past decade, which may have resulted in northward distribution shifts of sardine and other species (Muhling et al. 2020; Free et al. 2023). A recent projection study by Koenigstein et al. (2022) suggests that sardine biomass is likely to recover over the coming decades and may therefore support a fishery again. Understanding how habitat-based assignments of survey catches and fisheries landings may be impacted by both heatwaves and future climate change is thus extremely important.

In this study, we develop a conceptual model of sardine subpopulation distribution in the CCS that approximates current management assumptions. As previous research has focused primarily on environmental associations of the northern subpopulation in US waters, we expand these studies to better define sardine habitats across a broader latitudinal range, from the Baja California peninsula to British Columbia. We then examine the impacts of marine heatwaves and projected long-term climate change on the availability of putative subpopulations to three West Coast fishing ports and discuss the continuing robustness and practicality of separating subpopulations using only habitat-based assignments.

2 | Methods

2.1 | Biological Observations

Fishery-independent survey observations were compiled for sardine eggs, larvae, juveniles, and adults. These data were sourced from multiple different sampling programs (Table S1), as described below, with varying spatiotemporal coverage in the CCS (Figure 1).

2.1.1 | Eggs and Larvae

Egg and larval data were available from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program (covering the entire CCS), the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) program (covering Baja California), and multiple sampling programs conducted by the NOAA Northwest Fisheries Science Center (NWFSC: covering the northern CCS).

CalCOFI began in the 1940s as a response to the sardine collapse and has continued as a comprehensive ecosystem monitoring program (Gallo et al. 2019). It has occupied a standard grid of 66 stations off southern California since 1985, with other areas sampled periodically (McClatchie 2016). A

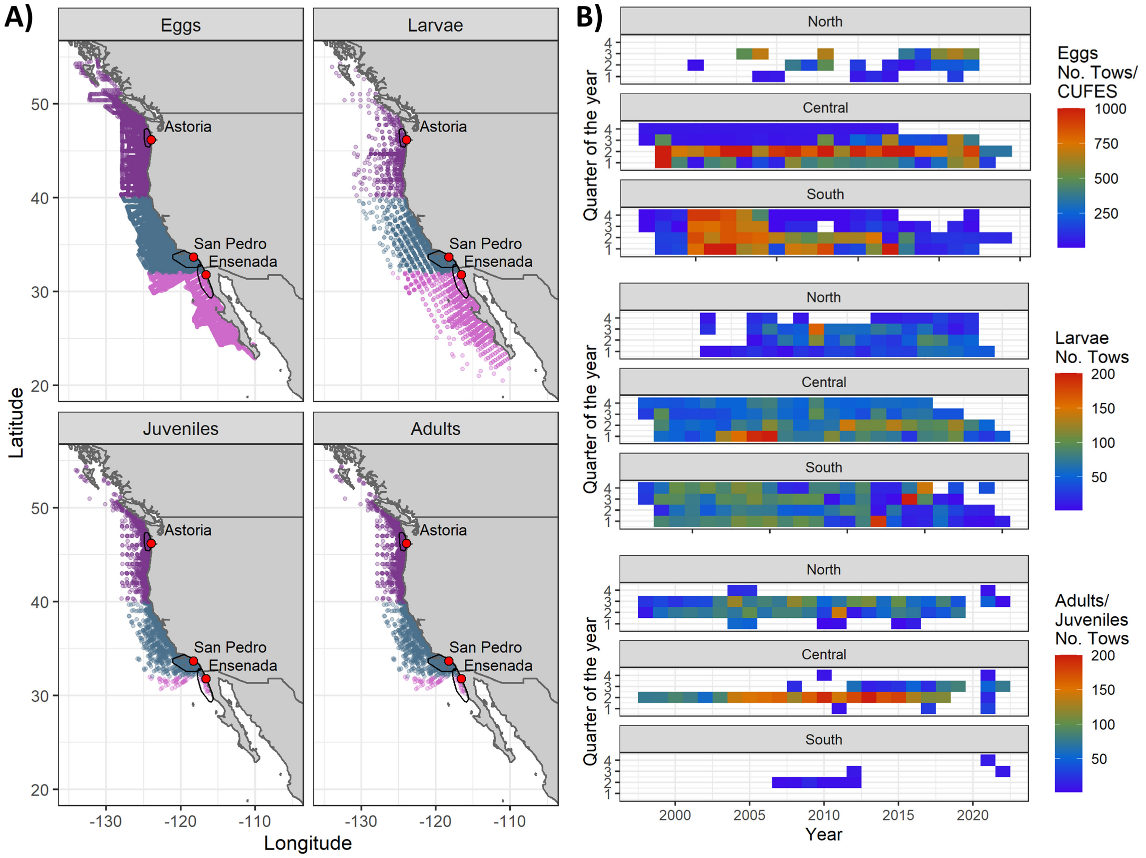

FIGURE 1 | (A) All sampling locations for sardine, color coded by region of the California Current (north = purple, central = green, south = pink). Note that regions are used to show overall sampling coverage, and do not correspond with putative sardine subpopulations. Fishing grounds associated with each port are also shown as black polygons. (B) Number of tows by region and quarter of the year by life stage. Egg sampling coverage (tows and CUFES) is shown in the top panel, larval sampling coverage is in the middle panel, and adult/juvenile sampling coverage at the bottom.

variety of gears have been deployed to sample fish eggs and larvae during this time. We obtained data on sardine egg distributions from 150 μm mesh plankton net tows covering the upper 70 m of the water column (Smith 1985) and from the Continuous Underway Fish Egg Sampler (CUFES; Checkley et al. 1997). CUFES can continuously sample at 3 m depth while the research vessel is on station or underway. CUFES samples were available from 1996 to 2019, with data collected in April across all years and other months between January and September sampled in some years. Larval sardine observations were obtained from standard oblique 0.71 m diameter bongo nets, which are fitted with 505 μm mesh and towed to 210 m depth (Moser 2001; Asch 2015). CalCOFI egg and larval sardine data were available through 2020. Data were available for all months of the year, but with typically one cruise per season since 1999.

The IMECOCAL program has sampled off the coast of Baja California, Mexico, since October 1997 (Baumgartner et al. 2008; Valencia-Gasti et al. 2018). We obtained sardine egg distributions from this survey from standard oblique bongo net tows (1998–2017) and CUFES (2000–2013) and larvae from oblique bongo net tows (1997–2019), equivalent to those used by the CalCOFI program. Bongo net samples were available from all months of the year, with between 2 and 8 months sampled in each year. CUFES samples were available from January to November, with between 1 and 8 months sampled per year.

In the northern CCS, larval sardine records were sourced from multiple NWFSC sampling programs conducted between 1998 and 2018. Samples were available for all months of the year, with between 1 and 12 months sampled per year. These surveys used 0.6–1 m ring and bongo net tows fitted with 200–333 μm mesh towed to 20–100 m depth and sampled along the central Oregon coast (Auth et al. 2015, 2018; Thompson et al. 2019). Use of different sampling gears and tow patterns can bias estimates of larval abundance. Smaller larvae may be extruded through larger mesh nets, and tow patterns that are too shallow may under-sample larvae present deeper in the water column. However, sardine larvae are generally distributed at depths shallower than 50 m (Auth et al. 2007), and previous work suggests that extrusion is not a large source of bias between 333 and 505 μm mesh nets for other Clupeiform larvae (Johnson and Morse 1994). As our study only examines larval occurrence, rather than abundance, the use of different sampling strategies across surveys is not likely to be a large source of bias.

2.1.2 | Juveniles and Adults

Records of juvenile and adult sardine were obtained from the Rockfish Recruitment and Ecosystem Assessment Surveys (RREAS, covering the US CCS south of 42° N), the NWFSC Pre-Recruit trawl surveys (covering 40°–48° N), the Stock Assessment Improvement Program (SAIP) surveys (covering 44°–47° N), the NOAA Southwest Fisheries Science Center (SWFSC) acoustic-trawl surveys (covering the entire CCS), and the NWFSC Columbia River predator trawl surveys (covering the Columbia River area from 45°–47° N).

Juvenile sardine were defined as those < 100 mm in fork length, just below the minimum recorded length at maturity (Dorval et al. 2015). The SWFSC and Columbia River trawl surveys used a trawl net towed near the surface at night at a target speed of 3.5–4.0 knots (Emmett et al. 2005; Zwolinski and Demer 2012; Zwolinski et al. 2012). Samples were available from 1998 to 2022, covering months from March to October. The RREAS, Pre-recruit, and SAIP surveys also sampled at night but targeted midwater depths, with the headrope kept at approximately 30 m below the surface (Sakuma et al. 2006; Phillips et al. 2009; Brodeur et al. 2011, 2019). Data covered all months of the year, but most sampling was completed in May or June. We therefore pooled data from the SWFSC and Columbia River Predator trawl surveys ("surface trawls") and data from the RREAS, Pre-recruit, and SAIP surveys ("midwater trawls") in subsequent analyses.

For all surveys and life stages, we calculated the distance from each sampled observation to the North American coast and discarded stations sampled further from shore than any life stage of sardine was recorded (600 km). This primarily removed observations from a few far-offshore ichthyoplankton sampling cruises contained in the CalCOFI database. Overall, larval observations had the broadest spatial and temporal coverage of any life stage. The southern and central CCS were the most heavily sampled, but samples were available in the northern CCS in most seasons starting in 2006. Trawl observations of adults and juveniles were concentrated in spring in the central CCS, while egg observations were concentrated in the southern and central CCS.

2.2 | Environmental Associations

We extracted SST and surface chlorophyll for the sampling date and location of each biological observation described above. SST was extracted at native daily 0.25° resolution from the NOAA Daily Optimum Interpolation Sea Surface Temperature (OISST) product, Version 2.1, which covers the years 1981–present (Reynolds et al. 2007; Huang et al. 2021). Surface chlorophyll concentration was extracted from a 0.04167° resolution multi-sensor product developed through the Ocean-Colour Climate Change Initiative (OC-CCI), covering September 1997 to present (Sathyendranath et al. 2019). Chlorophyll was extracted within a 0.25° × 0.25° degree box surrounding each observed sampling location and from 8-day composites overlapping biological sampling dates to minimize data loss due to cloud cover. As the satellite chlorophyll record begins in September 1997, data for training species distribution models covered September 1997 through the most recent year available. Although other oceanographic characteristics have also been shown to influence sardine distribution in the CCS (e.g., Asch and Checkley 2013; Muhling et al. 2019), we focused only on SST and chlorophyll in this study. This approach maintained consistency with statistical models currently used to assign sardine catches from commercial fisheries and fishery-independent surveys to the northern subpopulation in the region (Zwolinski et al. 2011; Kuriyama et al. 2020). In total, 81,477 biological observation locations had both SST and chlorophyll data available (Table S1).

We explored the environmental space covered by each survey using simple two-dimensional probability density plots. These suggested that the surface trawl surveys were best for sampling adult sardine and oblique bongo net tows were the best for sampling early life stages (Figures 2 and S1). Adult sardine were much less common in midwater trawls, and these surveys also sampled a narrower range of environmental conditions (Figure S1). Juvenile sardine were not observed frequently enough to support development of a predictive model, but probability density plots suggested that they occurred within the environmental ranges of adults and early life stages (Figure S1).

Sardine early-life stages were reasonably well sampled by both plankton net tows and CUFES, but the oblique tows targeting larvae covered the broadest environmental ranges, had the most complete sampling coverage by season, and also had the best coverage in warmer waters, which have historically been under-sampled. We acknowledge that as pelagic larvae can be dispersed substantially beyond their initial spawned locations (e.g., Weber et al. 2015), that larval sardine habitat is likely to be broader geographically than true spawning habitat. However, our data show that while egg and larval sardine distributions are not identical, they occupy similar areas within environmental space (Figures 2 and S1).

2.3 | Historical Species Distribution Models

We used generalized additive models (GAMs: Wood 2006) to predict the probability of occurrence of larval and adult sardine using observations from 1997 to 2020 (larvae) and 1998 to 2022 (adults). We included all available observations of adult and larval sardine in the GAMs, regardless of which putative subpopulation they likely belonged to. GAMs are semi-parametric regression models that can account for non-linear relationships between covariates and dependent variables using smoothing functions. We built our GAMs in the *mgcv* package (Wood 2017) in R 4.1.2 (R Core Team 2021), using a binomial distribution. We followed Zwolinski et al. (2011) by using a tensor product smooth of SST and surface chlorophyll to predict the presence or absence of each life stage. Tensor product smooths are smooths of several covariates that can be constructed from tensor products of the bases used to represent smooths of one of the covariates and allow the inclusion of an interaction between covariates measured on different scales (Wood 2006). Surface chlorophyll was natural log-transformed before inclusion in the GAMs to reduce strong right-skewness. The number of knots (k) was restricted to 5 to ensure that modeled relationships remained biologically reasonable. Two GAMs were constructed for each life stage: one used only SST and chlorophyll as predictors, and one also included a cyclic cubic spline of month to capture seasonality in spawning and migration. Model skill was measured using the area under the receiver operating characteristic (ROC) curve (AUC) using the pROC package (Robin et al. 2011), and partial responses were visualized using the *gratia* package (Simpson 2022). Model residuals were assessed using QQ-plots in the *DHARMA* package (Hartig 2024).

There is currently no published model that distinguishes overall suitable sardine habitat from unsuitable or low probability habitat and that also divides suitable habitat into putative northern vs. southern subpopulation habitat. We therefore built a conceptual model to meet this objective. We used results from the adult and larval sardine GAMs to build a simple model of sardine subpopulation habitats in SST and chlorophyll space. This model was built to approximate current management and thus stock assessment assumptions regarding sardine subpopulations. The building of a new conceptual model was necessary because the environmental conditions associated with the putative southern subpopulation are currently not defined. Zwolinski and Demer (2023) describe the habitat model that is the basis of the current methods for assigning fisheries landings and survey-derived biomass estimates to the northern subpopulation. They used April egg distributions from the CalCOFI CUFES samples, assuming they covered northern subpopulation spawning habitat, and found that eggs were primarily located in waters with

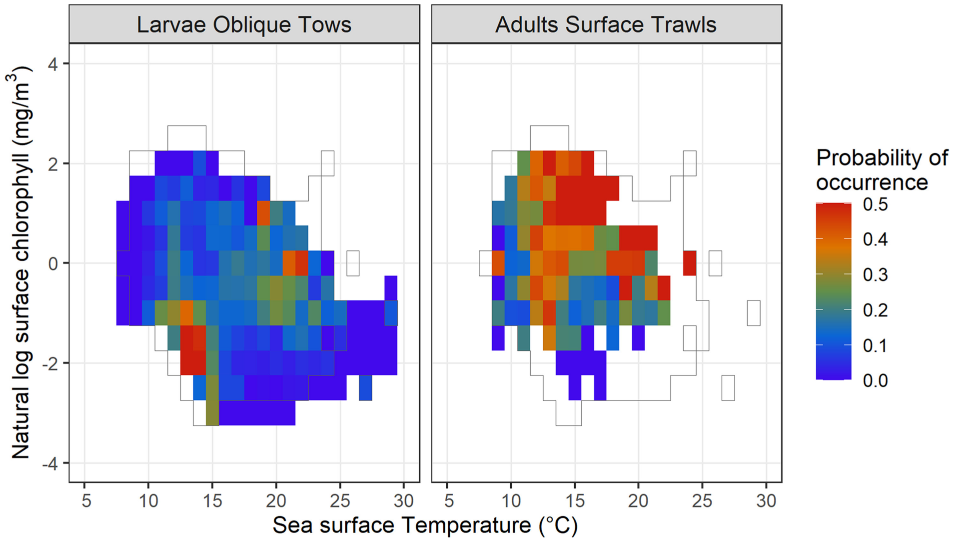

FIGURE 2 | Observed probability of sardine occurrence with respect to SST and surface chlorophyll. Left: early life history stages from oblique plankton net tows for larvae. Right: adult sardine from surface trawls (SWFSC CPS cruises and Columbia River plume predator surveys). The gray polygon encompasses all positive catch locations of any life history stage of sardine from any survey. Only cells with at least five observations available are shown.

SSTs from 11.5°C to 15.5°C and moderate surface chlorophyll concentrations of ~0.18–3.2 mg/m^3. At present, sardine caught in waters outside these ranges are assumed to be from the southern subpopulation, but the environmental conditions associated with these fish have not been examined. The conceptual model was restricted to the range of SST and surface chlorophyll conditions associated with biological observations.

Predicted values from the GAMs above 10% were defined as potentially favorable habitat. We initially completed this separation using only adult and larval GAMs containing month as a predictor but also compared these to results using GAMs without month. The 10% threshold encompassed 82% of stations with larval sardine present and 99% of stations with adult sardine present. This relatively inclusive cutoff was chosen to encompass the broad range of ocean conditions where sardine could potentially be collected, rather than focusing on core habitat or hotspots. Using alternative cutoff values (e.g., 5%, 20%) changed the distribution edges of key habitats but did not alter our overall conclusions. Environmental conditions where the probability of adult sardine occurrence was > 10% but the probability of larval occurrence was < 10% were categorized as "adult foraging" habitat. This category reflects that adult sardine in habitats not associated with early life stages are primarily foraging rather than reproducing but does not imply that adult sardine are not also foraging during spawning seasons.

Conditions where larval probability of occurrence was > 10% (regardless of adult presence) were defined as larval habitat. Results from the GAMs (see Section 3 below) were reasonably consistent with previous studies (e.g., Félix-Uraga et al. 2004), showing two incompletely separated peaks of larval occurrence in environmental space. While not asserting that these results confirm the existence of reproductively isolated subpopulations, we assigned different larval sardine habitats based on SST and chlorophyll conditions to reflect current management and stock assessment assumptions (e.g., Demer and Zwolinski 2014). We defined larval habitat in waters ≤16°C as "northern larval" habitat associated with the northern subpopulation and larval habitat ≥17°C as "southern larval" habitat. Larval habitat between 16°C and 17°C was defined as "undetermined larval" habitat, which was not possible to assign to either subpopulation with confidence. This "undetermined" range was based on uncertainty around previous cutoff values used for assigning sardine subpopulations (Zwolinski et al. 2011; Demer and Zwolinski 2014). Environmental conditions where the probability of both adult and larval occurrence was < 10% were defined as "low probability habitat."

2.4 | Marine Heatwave Indicators

We calculated port-specific marine heatwave indicators for three ports: Astoria (Oregon), San Pedro (California), and Ensenada (Baja California) for years 1981–2023 (Figure 1). These ports were chosen because they have historically been a focus for sardine landings, and each is assumed to interact with different subpopulations. Landings at Astoria are considered to be northern subpopulation only; San Pedro landings are primarily northern subpopulation, with some southern fish landed in warmer months; and Ensenada landings are considered to be a mix of northern and southern subpopulations depending on the season (Demer and Zwolinski 2014).

Environmental conditions were extracted within 100 km of each port for years 1981–2023 to encapsulate potential sardine fishing grounds and adjacent areas (see Section 2.5). We used monthly means of the NOAA 0.25° Daily OISST product, Version 2.1 (Reynolds et al. 2007; Huang et al. 2021) to define port-specific heatwave conditions. Following Jacox et al. (2020), we first linearly detrended SSTs to remove the warming signal since the late 1990s, calculated SST anomalies relative to a 1982–2011 climatology, and defined heatwave conditions as those exceeding the 90th percentile threshold, calculated for each month and port separately. As such, marine heatwaves are defined as anomalous warm events separate from the long-term warming signal (see Jacox 2019).

2.5 | Simulated Fishing Locations

We used simulated fishing locations to quantify the impacts of marine heatwaves and future climate change on the availability of sardine subpopulations to fishing ports. This was partially because a majority of the vessels targeting sardine in the CCS are not required to submit logbooks detailing catch dates and precise fishing locations. In addition, most sardine fisheries in US waters have been closed since 2015, and so few fishing records are available during recent strong marine heatwaves. Simulated fishing locations were random points in at least 30 m of water, within published areas of highest fishing effort, sourced from the Pacific Fisheries Information Network (PacFIN) for San Pedro, McCrae (2001), Wargo and Hinton (2016) for Astoria, and from INAPESCA (2023) for Ensenada (Figure 1). Two simulated vessels fished within the fishing area associated with each port each day, consistent with long-term records of approximate fishing effort from PacFIN. Trips typically do not last longer than a day due to the need to process fish while relatively fresh (Quezada et al. 2023). For recent historical analyses, simulated locations were calculated for all months at San Pedro and Ensenada, but only for June through November for Astoria, based on months where landings have been reported in the past (PacFIN; Demer and Zwolinski 2014). For future projections we examined all months for each port to allow for potential extension of the fishing season under climate change conditions. SST and surface chlorophyll were extracted for each simulated fishing location and used to assign each location to a sardine habitat type, using results from the GAMs and conceptual model described above.

2.6 | Future Projections

To determine future changes in sardine habitat availability to West Coast fisheries, we examined both long-term trends and higher frequency variability around these trends. Sardine habitat extent was then compared between (1) historical mean conditions, (2) historical heatwave conditions, (3) future mean conditions, and (4) future heatwave conditions.

Projections of future conditions in the CCS were sourced from an ensemble of dynamically downscaled earth system models

(ESMs). Pozo Buil et al. (2021) downscaled three ESMs selected to span the range of plausible futures for the CCS from Phase 5 of the Coupled Model Intercomparison project (CMIP5): the Geophysical Fluid Dynamics Laboratory (GFDL) ESM 2M, Institut Pierre Simon Laplace (IPSL) CM5A-MR, and the Hadley Center (HAD) HadGEM2-ES. A CCS configuration of the Regional Ocean Modeling System (ROMS) coupled to a biogeochemical model (NEMUCSC) was used for downscaling (Cheresh and Fiechter 2020). The ROMS domain spans 30°–48° N and inshore of 134° W, with 0.1° horizontal resolution and 42 terrain-following vertical levels (Veneziani et al. 2009). Each ESM was downscaled for the period from 1980 to 2100 using historical forcing (1980–2005) and the RCP8.5 high emission climate change scenario (2006–2100). Of the three downscaled ESMs, the GFDL model showed the weakest warming, the HAD model the strongest, and the IPSL model projections were intermediate between GFDL and HAD. For simplicity, we focus primarily on projections from the IPSL model (intermediate case, representative of the CMIP5 ensemble mean for RCP8.5) in this study. However, results from the GFDL and HAD models were similar, with slightly stronger/earlier changes in the HAD model and slightly weaker/later changes in the GFDL model, consistent with the rate of warming projected by each. Note that the lower warming rate in GFDL places it at approximately the mean warming among CMIP5 models under the RCP4.5 scenario, so this run serves as a useful proxy for a lower emissions scenario relative to the high emissions RCP8.5 scenario. SST and surface chlorophyll within fishing areas associated with each fishing port were extracted for each year and month from the downscaled ESM and used to define sardine habitats available to fishers from each port through to 2100, using results from the GAMs and conceptual model described above.

Substantial warming of the CCS is projected through to 2100 (Pozo Buil et al. 2021). However, short-lived events where temperatures are substantially "warmer than normal" (i.e., marine heatwaves, El Niño events) will continue to occur. Following Jacox (2019) and Amaya et al. (2023), we identified future marine heatwaves using a shifting baseline. We first removed long-term warming from ESM projections using a simple quadratic trend (which in practice was fairly close to linear). We then calculated monthly temperature anomalies with the long-term trend removed and defined future marine heatwaves in the same way as for the past (using a monthly 90th percentile threshold).

3 | Results

3.1 | Historical Species Distribution Models

The GAMs showed that larval sardine were associated with SSTs between 10°C and 26°C and a broad range of surface chlorophyll concentrations (Figures 2 and 3). Larval occurrences showed two peaks: one at ~10°C–15°C and one at ~19°C–26°C. However, both probability density plots of observations and predictions from the GAM suggested that these two peaks are incompletely separated (Figures 2 and 3). Month was highly significant to the larval GAM and was responsible for a large proportion of the model skill, reflecting the seasonal nature of sardine spawning (Table S2). In contrast, month was not as influential to the adult sardine GAM. There was also no evidence of distinct habitat groups for adult sardine. GAM partial responses to SST and chlorophyll remained similar in GAMs with month excluded. Uncertainty in predictions was highest near the edges of sampled environmental space and during spring and fall for adult sardine (Figure 3). Model skill was good for the larval GAM with month included (AUC = 0.82), fair for the larval GAM without month (AUC = 0.71), and weaker for the adult GAMs (AUC = 0.68 with month, 0.67 without month).

The conceptual model combining GAM predictions for sardine larvae and adults showed that larval habitat was present at a broad range of SSTs and chlorophyll concentrations (Figure 4). However, putative northern subpopulation larval habitat was more seasonally constrained than for the southern subpopulation. Northern larval habitat primarily occurred from February to May, while southern larval habitat was present throughout the year. Adult foraging (i.e., non-spawning) habitat was also present in all months. A conceptual model based on predictions from GAMs without month included as a predictor showed a similarly broad association between larval occurrence and SST, with adult foraging habitat primarily in cooler, higher chlorophyll waters (Figure S2). As results of the GAMs showed no geographic or environmental grouping or separation of adult foraging habitat across putative subpopulations, adult foraging habitat should be considered as mixed with respect to subpopulations.

We mapped habitats from the conceptual model in space for several example years to compare them with field observations and assess their spatial continuity and biological realism. Although simplistic, the conceptual model aligned with field observations reasonably well (Figure 5). Sardine eggs and larvae were common off California and Baja California in spring within larval habitats. While we did not model sardine egg distributions explicitly (see Section 2), observations of sardine eggs help to confirm the general boundaries of early life stage habitats. In 2011, there was a noticeable gap between two hotspots of egg and larval distribution off central California and the central Baja California peninsula, while in other years, early-life stages were more continuously distributed in the southern CCS. The approximate latitude of undetermined larval habitat, which separates northern and southern habitat, varied interannually from near the central Baja California peninsula in 2011 to the Southern California Bight in 2005. In summer, larvae were still commonly collected off Baja California, Baja California Sur, and in the Southern California Bight, within assumed southern habitat (Figure 5). Adult foraging habitat covered the remainder of the coastal CCS. A few scattered eggs and larvae were also collected in the northern CCS during summer in some years. These occurrences reflect the fact that adult foraging habitat was defined as conditions where the probability of larvae was < 10% (i.e., not zero). While the magnitude of the northern CCS spawning appeared much lower than in the southern CCS, the presence of eggs and larvae off Oregon and Washington highlights the potential spatiotemporal flexibility of sardine spawning behavior.

3.2 | Historical Impact of Marine Heatwaves

Simulated fishing activity between 1997 and 2022 overlapped with different sardine habitats depending on port and on whether marine heatwave conditions were present (Figures 6

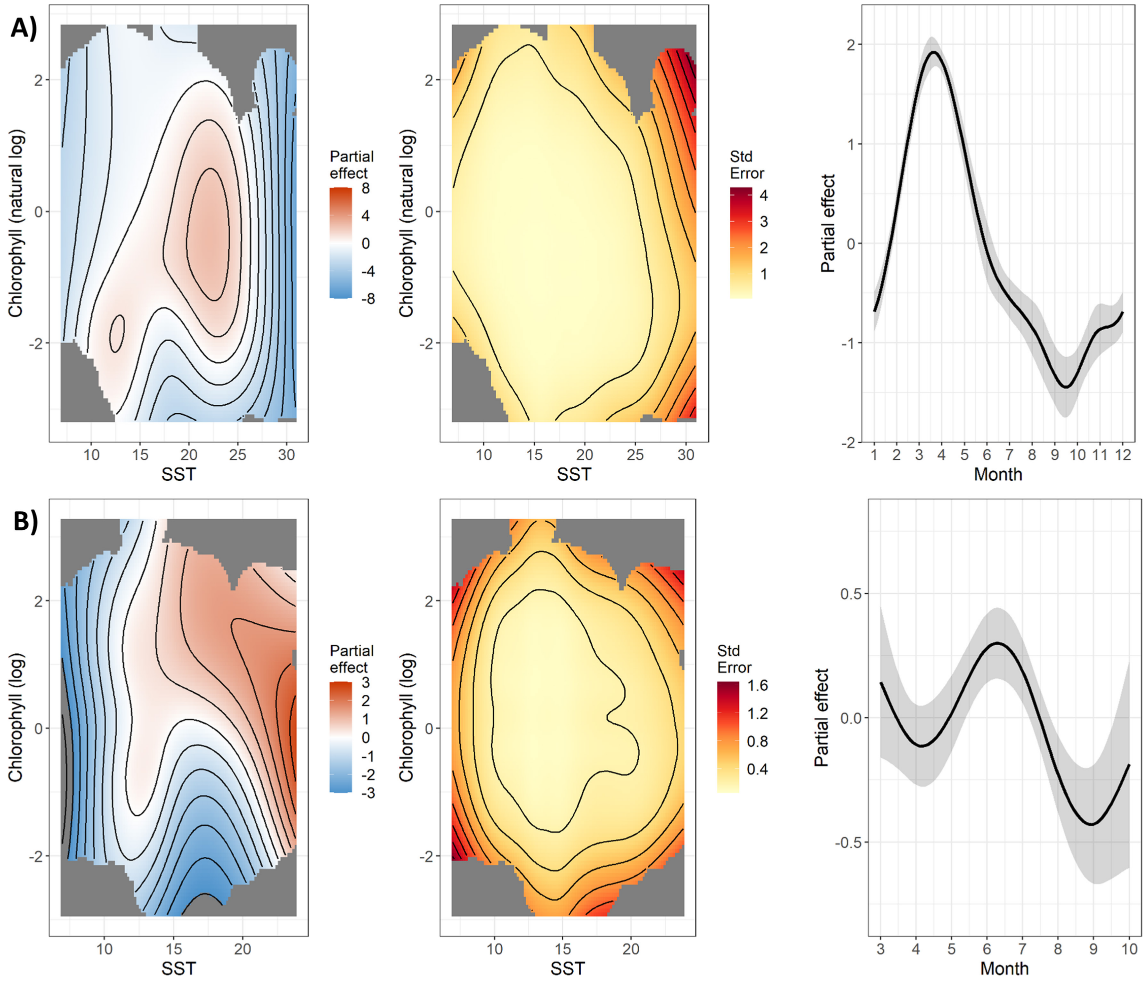

FIGURE 3 | Partial effects plots for generalized additive models for tensor product spline of SST and surface chlorophyll (natural log transformed) interaction, and cyclic cubic spline of month. (A) GAM predicting larval occurrences, (B) GAM predicting adult occurrences. Standard error surfaces are also shown in middle panels. Larger values indicate greater uncertainty in predictions. Environmental space not covered by the model training data is masked in dark gray in the left and middle panels.

and S3). For example, during January, fishers near San Pedro and Ensenada were primarily able to access adult foraging habitat during non-heatwave conditions (>95% of simulated fishing locations). In contrast, during marine heatwave conditions, simulated January fishing locations near Ensenada were in adult foraging habitat 77.8% of the time and in southern larval or low probability habitat the rest of the time. Fishing locations near San Pedro remained primarily within adult foraging habitat during MHWs (94.1%). From February to May, larval habitat was dominant off San Pedro and Ensenada. However, the putative subpopulation available differed. During non-heatwave conditions, simulated fishing locations in April were in northern larval habitat most of the time (87.9% off San Pedro and 59.9% off Ensenada). During marine heatwave conditions, fished locations overlapped with northern habitat less commonly (60.6% San Pedro, 1.7% Ensenada), and the proportion of effort in southern larval habitat increased (to 17.2% near San Pedro and 73.3% off Ensenada). During summer, adult foraging habitat dominated off Astoria, and most vessels fishing out of San Pedro or Ensenada overlapped with either adult foraging habitat or southern larval habitat. During marine heatwave conditions, the overlap with southern larval habitat increased (from 50.2% to 65.7% off San Pedro in July and from 47.0% to 79.4% off Ensenada). It is notable that during July, fishing activity off Astoria could occasionally overlap with southern larval habitat (Figure 6). Some sardine eggs and larvae have been recorded near Astoria during summer (e.g., July–August 2014: Figure 5). However, although these observations confirm that this habitat can support spawning, southern subpopulation fish are unlikely to be located in this area, based on current assumptions about their movement patterns.

3.3 | Future Projections

The IPSL ESM projected future substantial changes in the availability of sardine habitats to each of the three fishing ports (Figure 7). This availability was impacted both by long-term warming and periodic marine heatwaves. During the historical period, adult sardine were typically available throughout the CCS in January, April, and July, with northern subpopulation larval habitat widespread during April. By the end of the century, adult foraging habitat was still projected to be widespread in the CCS during cooler months. Most of the CCS was projected to be suitable for sardine larvae in April, but waters off San Pedro and Ensenada moved from largely northern subpopulation habitat

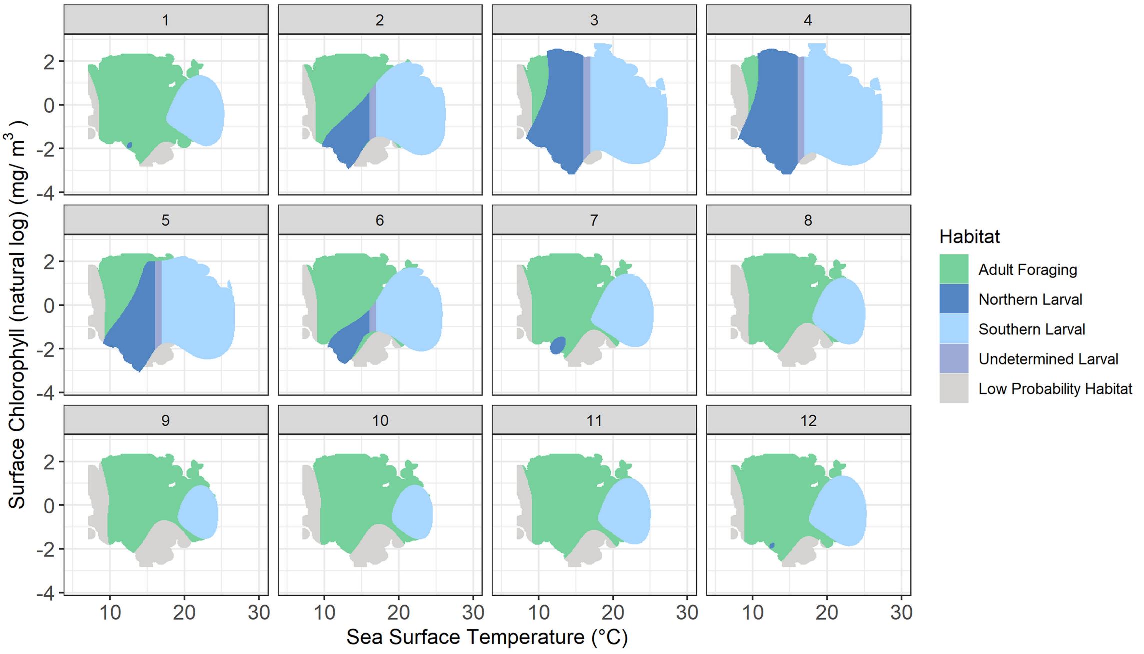

FIGURE 4 | Conceptual model of habitat partitioning for larval and adult sardine by month informed by GAMs predicting the presence of larval and adult sardine from SST, surface chlorophyll, and month. Habitat was defined as adult foraging if probability of adult occurrence was > 0.1 and probability of larval occurrence was < 0.1, northern larval if probability of larval occurrence was > 0.1 and SST was < 16°C, southern larval if probability of larval occurrence was > 0.1 and SST was > 17°C, undetermined larval if probability of larval occurrence was > 0.1 and SST was 16°C–17°C, and low probability habitat if probability of adult occurrence was < 0.1 and larval occurrence was < 0.1. Areas in white show conditions which were not represented by sampled observations. Subpanel heading shows month.

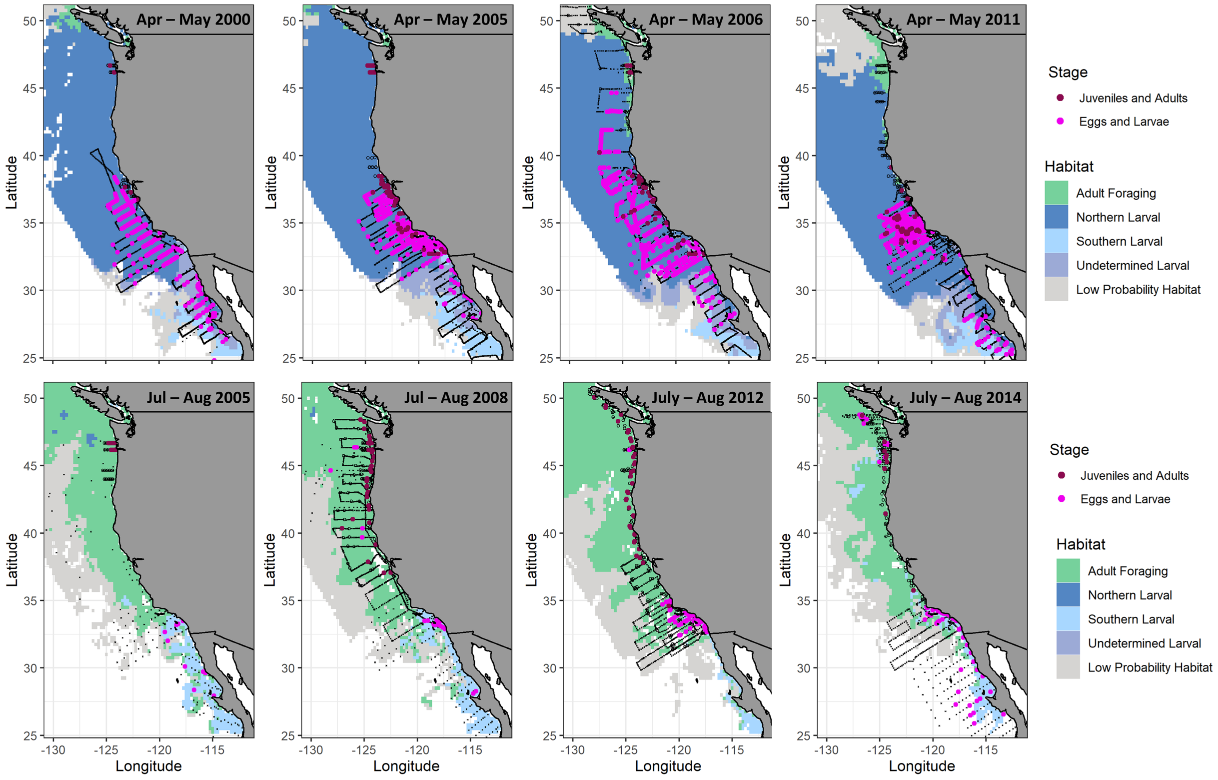

FIGURE 5 | Sardine habitat distribution from satellite data averaged over 2-month periods in selected years with higher coverage of observations. Spring (April–May mean: top) and summer (July–August mean: bottom) maps are shown. Egg and larval observations are combined from egg tows, CUFES, and larval plankton net tows, juvenile and adult observations are combined from surface and mid-water trawl surveys. "+" denotes negative egg or larval sampling location, and "o" denotes negative juvenile or adult sampling location. White pixels show areas > 600 km from the coast, as well as areas where surface chlorophyll data were not available due to cloud cover.

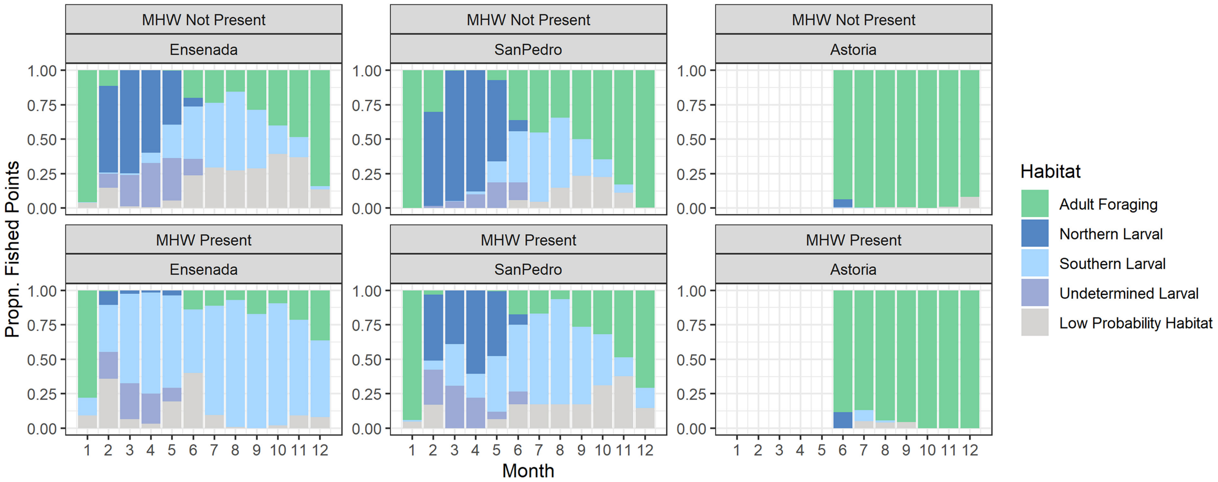

FIGURE 6 | Monthly prevalence of sardine habitats at simulated fishing locations near the ports of Ensenada, San Pedro, and Astoria. Top: during non-heatwave conditions, bottom: during heatwave conditions. Months January–May are masked for Astoria, as historically very few sardine have been landed during these months (< 0.1 metric tons total since 1981).

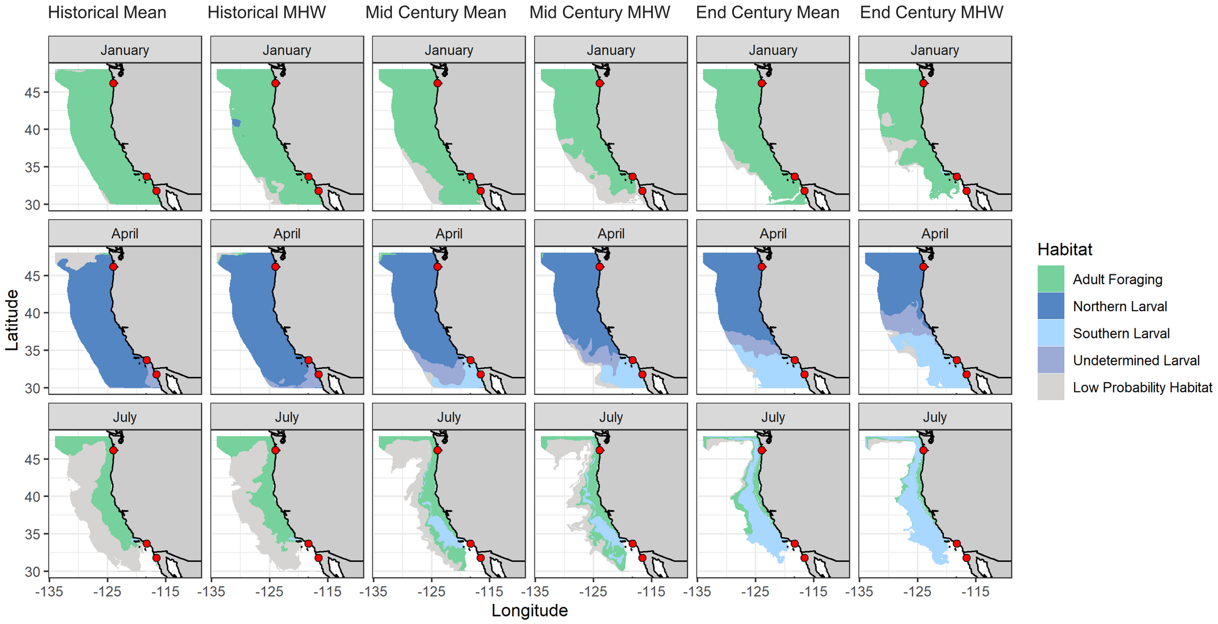

FIGURE 7 | Distribution of sardine habitats for historical (1980–2000), mid-century (2040–2060), and end-century (2080–2100) time periods under projections from the IPSL earth system model, for the months of January, April, and July. Habitat distributions under marine heatwave conditions are also shown, defined as years and months where at least 1 of the 3 fishing ports were experiencing a MHW. The ports of Ensenada, San Pedro, and Astoria are shown in red. Areas in white show conditions which were not represented by sampled historical observations.

to largely southern subpopulation habitat. By the end of the century, warming temperatures resulted in a shift from adult foraging habitat not associated with spawning to southern larval habitat. Marine heatwave conditions towards the end of the 21st century exacerbated these trends. Projections showed a further northward shift in the boundary between southern and northern subpopulation habitat in April and increasing occurrence of novel environmental conditions off San Pedro and Ensenada during July.

Results suggested an increasing prevalence of southern larval habitat off the two southern ports in the future. By the end of the 21st century, little to no northern larval habitat was projected to be present off either port (Figure S4). Off Astoria, the seasonal cycle of SST resulted in a switch between predominantly northern subpopulation habitat (< 16°C) from November to May and predominantly southern habitat from June to October. This pattern resembles present-day, non-heatwave conditions off San Pedro (Figure 6).

Time series of sardine habitat changes showed substantial variability in interannual habitat shifts across ports and months (Figure 8). For example, adult foraging habitat remained available near Astoria for the majority of the time series (1980–2100), with little interannual variability. In contrast, adult foraging habitat became gradually less available near Ensenada in January, but with high interannual variability. During April, a peak spawning month, larval habitat persisted near all three

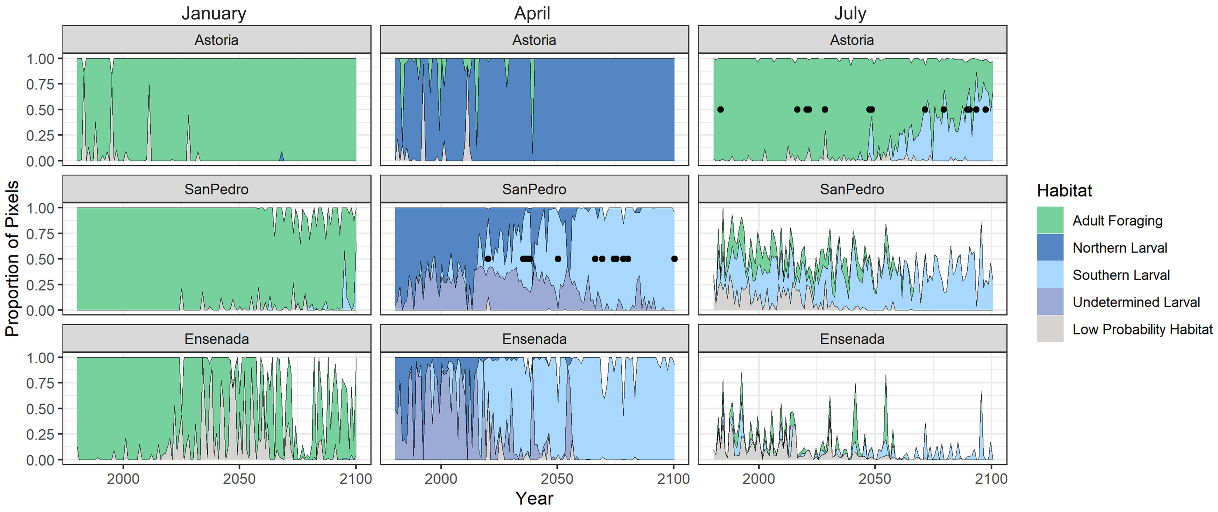

FIGURE 8 | Time series of annual sardine habitats under projections from the IPSL model, within fishing areas near the ports of Ensenada, San Pedro, and Astoria, for the months of January, April, and July. Areas in white show conditions which were not represented by sampled historical observations. Marine heatwaves near the port of San Pedro in April, and Astoria in July, are shown as black dots to demonstrate the impact of future heatwaves on sardine habitat availability when combined with more gradual warming.

ports but switched from being largely northern or undetermined larval habitat to largely southern habitat by 2050. Habitat off southern ports in July became increasingly novel, but with high interannual variability. It is not known whether these novel ocean conditions will continue to support sardine in the future, as fishery-independent surveys have not sampled analogous conditions in the past. The same time series analyses completed using the GFDL model were generally similar to those using IPSL but with slightly delayed transitions between habitats by port due to weaker warming (Figure S5).

The impact of marine heatwaves was dependent on the extent of underlying, climate-driven warming. For example, prior to 2050, marine heatwaves near San Pedro in April resulted in increased availability of southern larval habitat. After this time, ongoing warming resulted in a predominance of southern larval habitat, and so marine heatwaves no longer impacted sardine habitat availability to this port. Conversely, the occurrence of heatwaves prior to around 2040 did not change the sardine habitats available near Astoria in July. However, in the latter half of the 21st century, marine heatwaves became increasingly associated with the occurrence of southern larval habitat (Figure 8). Due to the modeled relationship between month and northern larval habitat, this transition is projected to occur without any northern larval habitat becoming available. In contrast, when the same time series were built using the GAMs that did not include month as a predictor (Figure S6), northern larval habitat was much more widespread, particularly in January (at all ports) and in July (off Astoria). These results highlight the need to better understand the triggers of spawning and migration in sardine and their ability to modify these phenologies when confronted with changing environmental conditions.

4 | Discussion

Results presented here combine data from extensive survey efforts across multiple decades to define oceanographic habitats associated with sardine occurrence. We use these data along with historical and projected oceanographic conditions to show that marine heatwaves can impact the availability of putative sardine subpopulations to fishing ports along the North American West Coast. In addition, a combination of climate-driven warming and marine heatwaves is expected to increase southern subpopulation larval habitat extent across a broader portion of the study region.

4.1 | Historical Habitat Distributions

In this study, we confirm the broad environmental and geographic ranges occupied by sardine along the North American west coast. Adults and early-life stages were recorded where SST was between 8°C and 29°C and where surface chlorophyll was oligotrophic ($<0.1\,\mathrm{mg/m^3}$) to highly productive ($>14\,\mathrm{mg/m^3}$). Within these ranges, observations and distribution models showed two incompletely separated hotspots for larval occurrence. One was characterized by SSTs cooler than approximately 16°C and lower chlorophyll concentrations and primarily occurred in spring. The other was characterized by SSTs warmer than ~17°C and occurred year-round. While this warmer larval habitat typically occurred off southern California and Baja California, some patches were also located in the northern CCS in summer during warmer years (e.g., Figure 5). These patterns are reasonably consistent with previous studies, such as Zwolinski et al. (2011) and Zwolinski and Demer (2023), who used egg collections to define environmental spawning habitat for the northern subpopulation only. They are also similar to the findings of Lluch-Belda et al. (1991), who examined sardine spawning and SST in the southern California Current. Our findings are also consistent with results from historical data collected when sardine were much more abundant and survey coverage was more comprehensive. These studies generally show seasonal spawning in the Southern California Bight and year-round occurrence of eggs and larvae further south off

Baja California (Hernandez-Vasquez 1994; Torres-Villegas et al. 1995; Tran 2023). However, the combination of data from the CalCOFI and IMECOCAL surveys in our study showed that egg and larval distributions were fairly continuous from the central Baja California peninsula to central California during spring, consistent with, e.g., Lluch-Belda et al. (2003). The occurrence of two hotspots for egg and larval occurrence in environmental space therefore did not translate to a strong geographic separation of putative subpopulation spawning areas in most years.

In contrast to larvae, distributions of adult sardine did not show any separation into multiple groups in environmental space. Mixing of juveniles and adults from distinct subpopulations on foraging and fishing grounds has been recorded for other pelagic species (Grewe et al. 2015; Rodríguez-Ezpeleta et al. 2019; Bekkevold et al. 2023), and so it is possible that any subpopulation structure in sardine may not be evident from environmental ranges associated with adults. However, if this behavior is occurring in sardine, separating out catches of northern subpopulation adults from fisheries and fishery-independent surveys using a habitat model trained on early-life stages may not be practical. It is not possible to determine from our results whether there are in fact separate, reproductively isolated subpopulations of sardine. However, while additional research on genetic structure, length compositions, and other lines of evidence is ongoing, sardine in the eastern North Pacific continue for now to be managed as two subpopulations, and habitat models will be used to separate out catches and biomass of the putative northern subpopulation.

Importantly, our results suggest that this uncertainty is likely to be magnified by changing ocean conditions. During marine heatwaves, southern larval habitat is more likely to be prevalent near San Pedro and Ensenada, as water temperature is more likely to exceed 17°C than during non-heatwave conditions. The CCS has been subject to a series of marine heatwaves since 2013, and water temperatures along much of the coast have been warmer than the long-term average since this time (Thompson, Bjorkstedt, et al. 2022). While directed fisheries for northern subpopulation sardine have been closed since 2015, acoustic-trawl surveys continue to monitor sardine biomass each year. Starting in 2016, a large proportion of sardine in the coastwide summer acoustic-trawl surveys were observed off of southern California. Based on the model of Zwolinski et al. (2011), these fish were assumed to be southern subpopulation (Yau 2023) and coincided with a strong increase in landings of putative southern subpopulation sardine off Baja California. In the years before 2016, the proportion of sardine from surveys in the US CCS assumed to be southern subpopulation was relatively low. This uncertainty in separating out northern subpopulation sardine has been identified as a key uncertainty in the stock assessment (Kuriyama et al. 2020), and our results suggest that this issue may be magnified during marine heatwaves and with ongoing climate change.

4.2 | Future Projections

Projections from this study suggest that sardine will continue to be available to eastern North Pacific fishing ports throughout the CCS in the future, despite substantial future warming (Pozo Buil et al. 2021). This finding agrees with other studies using more complex models (e.g., Petatán-Ramírez et al. 2019; Fiechter et al. 2021; Koenigstein et al. 2022). Sardine from the Gulf of California subpopulation currently support fisheries east of the Baja California Peninsula, where SSTs can seasonally exceed 30°C (Petatán-Ramírez et al. 2019), and critical thermal limits for Pacific sardine are > 29°C (Martínez-Porchas et al. 2009; Pribyl et al. 2016). Although we do not estimate future changes in recruitment, foraging conditions, stock productivity, or migration patterns, it appears likely that the CCS will continue to support sardine across much of its latitudinal range in the future (Petatán-Ramírez et al. 2019; Fiechter et al. 2021; Smith, Muhling, et al. 2021; Koenigstein et al. 2022).

The key projected future changes from our study instead relate to the availability of different sardine subpopulations to different nations and fishing ports through time. Habitat characteristic of the southern subpopulation will become more prevalent off San Pedro and Ensenada. By the mid-21st century under a high emissions scenario, mean SSTs within fishing areas associated with these two ports will exceed 16°C throughout most of the year, and SSTs will exceed 17°C nearly year-round by the end of the century. Under current habitat-based assignments, there will thus be no northern subpopulation sardine available near these two ports within the next few decades.

The situation near Astoria is more uncertain. Currently, all sardine fished in the northern CCS are assumed to be from the northern subpopulation, based on habitat conditions and expected migration behaviors. However, future projections show increased prevalence of southern subpopulation larval habitat near this port in the future. This change is largely due to the phenology of spawning forced by the inclusion of a month covariate in the GAMs: projections of future habitats off Astoria from the GAM without month show a transition from northern larval habitat to southern larval habitat through time. Laboratory studies suggest that both temperature and photoperiod are important for triggering spawning in sardine (Dorval et al. 2019), but it is not entirely clear how they interact to initiate spawning in the wild. As conditions in the northern CCS approach present-day cutoff values for northern subpopulation sardine, it will be essential to reevaluate whether current practices are sensible for more northern ports and survey locations. It will also be important to determine the precise drivers of sardine spawning, recruitment, and migration to better understand seasonal availability of different subpopulations and to assess whether current paradigms regarding migration and spatial separation of subpopulations are realistic.

Projections of future ecosystem states are often presented as multidecadal means to reduce the impact of internal interannual variability in climate models (Stock et al. 2011; Drenkard et al. 2021). While this approach effectively isolates the longer-term, externally forced climate change signal, it can obscure the fact that extreme events such as marine heatwaves will continue to occur in the future, even when viewed relative to the warmer future mean state (Jacox 2019). Similar to the present day, future marine heatwaves may lead to rapid distribution shifts in mobile marine species and require agile management responses (Jacox et al. 2020; Spillman et al. 2021). Our results show that where conditions are near cutoff points between different habitats, marine heatwaves will continue to drive interannual variability in spatial availability of sardine habitats. Thus, fisheries assessment and management frameworks will need to be robust to a combination of gradual warming and shorter-lived marine heatwaves.

4.3 | Study Caveats and Limitations

While the results from the current study expand current knowledge of past and future sardine distribution in the CCS, there are several important limitations to our work. Firstly, our distribution models were highly simplistic, relying only on SST, surface chlorophyll, and month at broad spatial and temporal scales. While previous studies have found these predictors to be of high importance in determining sardine distributions (e.g., Muhling et al. 2019; Petatán-Ramírez et al. 2019), sardine life history is complex, and the phenology of their movement and spawning clearly responds to other drivers not included here. In particular, the relative importance of temperature, day length, overall abundance, food availability, and other cues is not clear. This is a key knowledge gap for future projections, as SST will change markedly in the future while day length will not. Our framework also relied on simple simulated fishing behaviors, while socioeconomic studies show that fisher responses to changing ocean conditions and species availability can be complex (Quezada et al. 2023).

In addition, while tagging studies have shown that adult sardine can move substantial distances in the CCS (Clark and Janssen 1945), it is not known how plastic this behavior is in response to environmental cues or population size. Our MHW indicator did not distinguish between longer-lived, ecosystem-wide MHWs versus shorter events resulting from, e.g., El Niño conditions, and it is not clear how MHW persistence impacts sardine responses. Renewed tagging efforts using modern mark-recapture equipment could be valuable for resolving this issue. It is also not clear whether migration behaviors in putative northern and southern population fish result in consistent spatial separation of adult fish, and if so, whether such a separation will continue in the future.

Our models also do not consider changes in recruitment or stock productivity or interactions between these factors and species distributions. While mechanistic models are increasingly being used to produce future projections of sardine distribution and biomass in the CCS, to date these studies have dealt only with the assumed northern subpopulation, roughly within the US Exclusive Economic Zone (e.g., Fiechter et al. 2021; Koenigstein et al. 2022). We also note that while the climate projections used in this study follow best practices for dynamical downscaling, there may still be substantial biases in the temperature and chlorophyll fields (Pozo Buil et al. 2021). Lastly, while expansive and high-quality data collection programs were critical to the current study, sampling coverage for adult sardine was much patchier in environmental and geographic space than for early life stages. We also note that additional survey data from Mexican and Canadian waters would be extremely beneficial. In particular, our distribution models were more uncertain within warmer waters, and we were not able to clearly define upper temperature limits for either larval or adult sardine.

5 | Conclusions

Overall, our results show that adult and larval sardine occupy a broad range of oceanographic habitats in the CCS. While larval distributions can be incompletely separated into two groups based on temperature and chlorophyll, adult distributions are more continuous in geographic and environmental space. Recent marine heatwaves resulted in greater prevalence of southern subpopulation and "undetermined" habitat in US waters, and this pattern is likely to continue with ongoing anthropogenic warming. Current stock assessment and management frameworks may be challenged by these shifts. Increased understanding of sardine ecology, subpopulation structure, movement, and migration, as well as enhanced biological monitoring, will be key for ensuring climate resilience of CCS sardine fisheries.

Author Contributions

Study conception and design: Barbara Muhling. *Data collection and curation:* Juan Zwolinski, Toby Auth, Richard Brodeur, Sylvia Jiménez Rosenberg, Gerardo Aceves-Medina, and Jose Augusto Valencia Gasti. *Methodology:* Barbara Muhling, Juan Zwolinski, Mercedes Pozo Buil, Michael Jacox, Jerome Fiechter, Richard Brodeur, Felipe Quezada Escalona, and Desiree Tommasi. *Formal analysis:* Barbara Muhling. *Funding acquisition:* Peter Kuriyama, Desiree Tommasi, Sylvia Jiménez Rosenberg, and Gerardo Aceves-Medina. *Project administration:* Peter Kuriyama. *Interpretation of results:* All authors. *Writing – original draft:* Barbara Muhling. *Manuscript edits:* All authors. All authors reviewed the results and approved the final version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

NOAA Optimum Interpolation (OI) SST V2 data, the Ocean Colour Climate Change Initiative dataset, Version 6.0, egg and larval data from CalCOFI, trawl data from the NOAA Southwest Fisheries Science Center trawl surveys, and the Rockfish Recruitment and Ecosystem Assessment Surveys are freely available on the NOAA Coastwatch ERDDAP server at https://coastwatch.pfeg.noaa.gov/erddap/index.html. Egg and larval data from the IMECOCAL Program are available upon reasonable request to Dr. Jiménez-Rosenberg. Other survey data are available upon reasonable request to the corresponding author.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.