

The potential impact of a shifting Pacific sardine distribution on U.S. West Coast landings

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Abstract

Many fish species are shifting spatial distributions in response to climate change, but projecting these shifts and measuring their impact at fine scales are challenging. We present a simulation that projects change in fishery landings due to spatial distribution shifts, by combining regional ocean and biogeochemical models (forced by three earth system models, ESMs: GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-MR), correlative models for species distribution and port-level landings, and a simulation framework which provides realistic values for species abundance and fishery conditions using an historical “reference period”. We demonstrate this approach for the northern subpopulation of Pacific sardine, an iconic commercial species for the U.S. West Coast. We found a northward shift in sardine landings (based on the northern subpopulation’s habitat suitability), with projected declines at southern ports (20%–50% decline by 2080) and an increase (up to 50%) or no change at northern ports, and this was consistent across the three ESMs. Total sardine landings were more uncertain, with HadGEM2 indicating a 20% decline from 2000 to 15 levels by 2070 (a rate of 170 mt/y), IPSL a 10% increase (115 mt/y), and GFDL an 15% increase by the year ~2050 followed by a sharp decrease. The ESMs also differed in their projected change to the timing of the fishing season and frequency of fishery closures. Our simulation also identified key constraints on future landings that can be targeted by more tactical assessment; these included the seasonality of quota allocation and the abundance of other species in the catch portfolio.

KEYWORDS

California Current, climate vulnerability, ROMS, species distribution model

1 | INTRODUCTION

Impacts of climate change on marine life include changes to their spatial distribution, productivity and phenology (Free et al., 2019; Pinsky et al., 2013; Poloczanska et al., 2013). Distribution shifts are predicted or already underway for many marine species (Nye et al.,

2009; Perry et al., 2005) and are expected to contribute to large-scale redistribution of global fishery catch potential (Cheung et al., 2010). Species may shift their distribution outside historical fishing areas, or across national boundaries (Ishimura et al., 2013), resulting in changes to catch and catch composition (Pinsky & Fogarty, 2012; Sumaila et al., 2011). The timing of fishing seasons may also

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change as, for example, the timing of species migrations changes (Peer & Miller, 2014; Sims et al., 2001). Projecting species distributions and the potential impacts on fisheries is a valuable component of climate change risk assessment (Hazen et al., 2013; Rogers et al., 2019; Selden et al., 2019), aimed ultimately at building resilience in management strategies and coastal communities (Miller et al., 2018; Sumaila et al., 2011).

On the U.S. West Coast, future changes to ocean conditions are projected to lead to relatively strong northward distributions shifts of some marine species (Cheung et al., 2015; Morley et al., 2018). Without adaptation, fishing communities may face declining fishing opportunities, and fleets with smaller spatial extent may be particularly at risk from shifts in species distribution (Rogers et al., 2019; Selden et al., 2019). Expected changes extend to the productivity and spatial distribution of forage fish, such as Pacific sardine *Sardinops sagax* (Checkley et al., 2017; Cheung et al., 2015; Morley et al., 2018), and the sardine fishery may be particularly sensitive to distribution shifts as it occurs predominantly near-shore, with vessels typically returning daily to land their catch.

Pacific sardine is an iconic commercial species for the U.S. West Coast and has a long history of large fluctuations in abundance (Baumgartner et al., 1992). The abundance, productivity and distribution of sardine are closely linked with environmental and climate conditions, but the mechanisms driving sardine boom and bust dynamics remain unclear (Deyle et al., 2013; Jacobson & MacCall, 1995; Lindegren et al., 2013; McFarlane et al., 2002). There are three subpopulations of sardine in the California Current system (CCS), with the northern subpopulation the primary focus of U.S. management (Hill et al., 2018) and the focus of this study. The distribution of the northern subpopulation ranges between northern Baja California and British Columbia and is strongly influenced by temperature (Emmett et al., 2005; Kaplan et al., 2016; Zwolinski et al., 2011). This subpopulation also exhibits a variable latitudinal migration, dependent on habitat suitability as well as population size and age structure (Barange et al., 2009; Demer et al., 2012; McDaniel et al., 2016). A recent marine heatwave in the CCS was associated with an earlier sardine spawning and an unprecedented northern shift of the spawning area (Auth et al., 2018; McClatchie et al., 2016). A further shift in sardine distribution in the future appears likely (Morley et al., 2018), as is underway for other small pelagic fishes (Checkley et al., 2017). A key question, then, is how a distribution shift of the northern subpopulation may impact landings, given expected changes to ocean temperatures and upwelling in the CCS.

There are numerous challenges in projecting spatial distributions and fishery landings, especially for a “boom-bust” species such as sardine, with uncertainty stemming from climatic, biological, and social-economic processes (Cheung et al., 2016; Morley et al., 2018). Uncertainty in future climate is typically handled using projections from multiple climate models and/or future emissions scenarios (Knutti & Sedláček, 2013), and fine-scale regional ocean models are increasingly available for many coastal areas. In terms of biological processes, correlative species distribution models (SDM) has been

successful for evaluating fishery impacts by measuring changes in spatial distribution over fishing grounds (Rogers et al., 2019; Selden et al., 2019), and although these models can account for species abundance (Muhling et al., 2019; Rogers et al., 2019), projecting species abundance far into the future remains a great challenge. Incorporating social-economic processes is more complex still (Lam, 2019), and projecting these systems ultimately relies on coupled end-to-end frameworks, with a general approach of scenario testing (Hollowed et al., 2020; Lindegren et al., 2010; Marshall et al., 2017). Clearly, long-term projection of climate impacts on fishery landings is immensely challenging, yet the value of such projections motivates development of alternative approaches to help identify these impacts.

Our approach was to use a correlative model to relate port-level landings to sardine probability of presence from a sardine SDM and then project this presence to quantify future changes in landings. To project sardine presence, we used a regional ocean model with biogeochemistry for the CCS, forced by output from multiple earth system model (ESM) projections (Poza Buil et al. accepted). The key development of our approach was to use an historical “reference period” for all other components of the system, namely sardine abundance and influential covariates of landings (such as port capacity). This avoided the great challenge of projecting species abundance and fishery changes while allowing us to isolate the effect of a shifting spatial distribution on landings. By using multiple ESMs, we incorporated uncertainty in climate projections, and by using a reference period and a simulation framework, we created a likely range of landings based on recent observed variation in sardine biomass as well as key fishery and management conditions. Projections of species distributions and catch potential have often relied on relatively coarse resolution environmental information (Cheung et al., 2015; Hazen et al., 2013), while our dynamical downscaling approach increased the horizontal resolution by an order of magnitude to 0.1° (~10 km). These high-resolution models enable representations of near-shore oceanographic processes such as upwelling and their biogeochemical impacts, which are key drivers of the distribution of coastal species like Pacific sardine (Checkley et al., 2017), and enable distribution modelling on fine, port-relevant, spatial scales.

Our goal was to quantify the potential impact of a shifting sardine distribution on landings and compare how this impact varied across three ESMs projecting potential future climate and ocean states. Our specific aims were to: (1) quantify how a changing spatial distribution of the northern subpopulation of sardine may impact U.S. landings out to 2080; and (2) identify influential correlates of sardine landings and evaluate which act as management-relevant constraints to future landings. Given our approach is based on correlative models, the actual processes driving changes in distribution and landings are unknown; thus our focus was on estimating the scale of impact due to changes in spatial distribution, and identifying possible climate sensitivities in the fishery worth investigating through tactical modelling approaches (such as management strategy evaluation) over shorter time frames.

2 | METHODS

Our approach builds upon studies projecting future changes in species distribution over fishing grounds (Rogers et al., 2019; Selden et al., 2019) by considering how projected shifts in sardine habitat may affect port-level landings, while accounting for realistic conditions for sardine abundance and management constraints. Our analysis incorporated two correlative models and a simulation (Figure 1). The first model was a SDM describing the probability of presence of the northern subpopulation of Pacific sardine. The second was a landings model describing port-level landings as a function of sardine presence and additional fishery and port-level factors. The simulation used the landings model to predict port-level landings, while allowing for dynamic feedback between landings, annual catch limit (ACL) (quota) allocation and fishery closures. The simulation was first run for 2000–15 to evaluate goodness-of-fit, and then for 1980–2095 to evaluate possible change in sardine landings due to projected shifts in sardine habitat suitability based on a small ensemble of regional ocean projections. Sardine dynamics are characterized by boom and bust cycles, but the specific environmental drivers of these fluctuations are not completely understood, making projection of the response of sardine biomass to future climate change difficult. To avoid the challenge of projecting sardine biomass and fishery/management dynamics, we projected ocean conditions and associated sardine habitat suitability only, and used 2000–15 as a “reference period” to provide all other information. In short, our approach estimated how sardine landings would respond to future climatic conditions and subsequent spatial distribution of sardine,

given the sardine biomass and associated catch limits of the 2000–15 period.

2.1 | Species distribution model

We used an SDM developed for the northern subpopulation of Pacific sardine, as presented in Muhling et al. (2019, 2020). The model is a boosted regression tree (BRT; Elith et al., 2008) fitted to presence–absence data from a trawl survey. The trawl survey was conducted by the NOAA Southwest Fisheries Science Center, and the model was fitted to 1486 hauls from 2003 (when the survey began) to 2016. The survey occurred primarily in spring and summer (Zwolinski et al., 2012), which means the SDM represents the northern subpopulation (Muhling et al., 2019). Model covariates were 14 environmental variables (Table 1), as well as annual spawning stock biomass (SSB) which was taken from recent stock assessments of the northern subpopulation (Hill et al., 2014, 2018). By including SSB as a covariate, the SDM calculates probability of presence of sardine, given habitat suitability and sardine biomass. We chose to model probability of presence (instead of biomass or abundance) in our simulation, because this aligned with existing SDMs (Zwolinski et al., 2011) and because the abundance of sardine when present may be influenced by processes not well described by the scale of our ocean projections.

For model fitting, dynamic ocean covariates were sourced from a data-assimilative Regional Ocean Modeling System (ROMS) configured for the CCS (Neveu et al., 2016), and surface chlorophyll

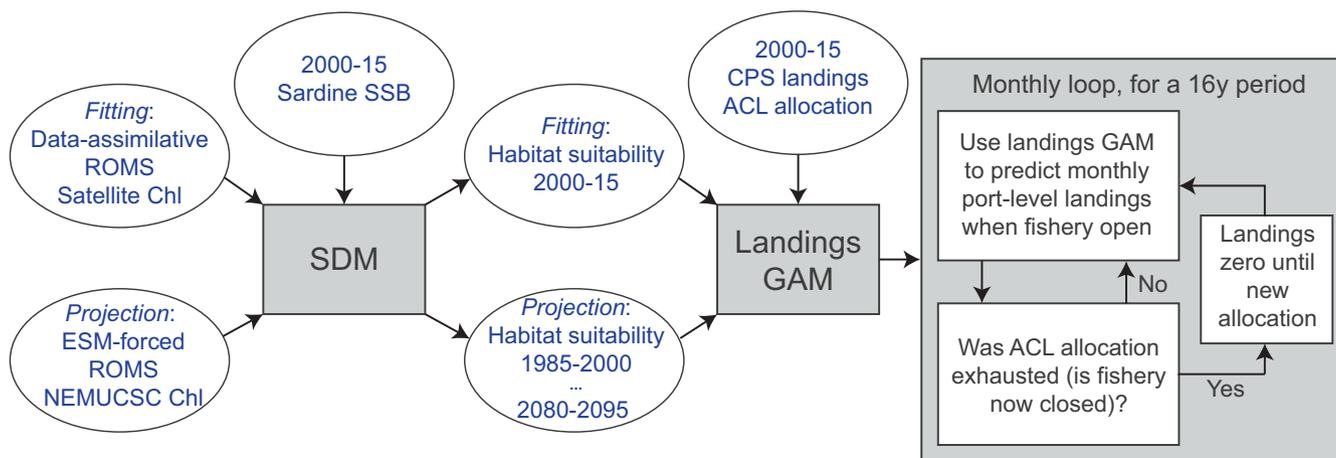


FIGURE 1 Schematic of the simulation's structure and inputs. A species distribution model (SDM) was used to predict sardine probability of presence, based on the environment (their habitat suitability) and sardine spawning stock biomass (SSB). A landings generalized additive model (GAM) used this probability of presence and other covariates to predict monthly landings. A simulation loop was used to estimate when cumulative landings reached an annual catch limit (ACL) allocation, at which point the simulated fishery was closed until a new allocation. The 2000–15 period was used to fit the GAM, using environmental data sourced from a data-assimilative Regional Ocean Modeling System (ROMS) and satellite chlorophyll (“Chl”). The same models were used to project sardine landings (from 1985–2095), but with environmental data sourced from ROMS and the biogeochemical NEMUCSC model forced by one of three Earth System Models (ESMs). The 2000–15 period was used as the “reference period” in our analysis, providing all information to predict sardine landings (SSB, ACL allocations, landings of other coastal pelagic species [CPS]), except for the projected habitat suitability. Thus, projections were done as 16-year time series (the duration of the reference period), beginning in every year from 1985 to 2080

TABLE 1 Summary of covariates and their sources for the Pacific sardine SDM (BRT; Muhling et al., 2019), and landings model (GAM)

Model	Covariate	Description	Source
BRT SDM	SST	Sea Surface Temperature (°C)	ROMS
	SSB	Spawning Stock Biomass (mt)	Stock Assessment (Hill et al 2014, 2018)
	Chl	Mean monthly surface chlorophyll (mg/m ³). 4th root transformed	Reference period: ocean colour product. Future period: NEMUCSC
	BV	Bulk buoyancy frequency (s ⁻¹). Represents stability of the upper water column	Derived from ROMS
	SST-sd	Standard deviation of SST (°C), at a scale of 0.3-degree resolution	Derived from ROMS
	SSH	Sea Surface Height (m)	ROMS
	Curl	Wind stress curl (N/m ³)	ROMS
	SU-str	Surface eastward wind stress (N/m ²)	ROMS
	EKE	Eddy Kinetic Energy (m ² /s ²). Log _e transformed	Derived from ROMS
	Lunar	Moon phase (proportion). This was fixed at 0.5 for prediction	"lunar" R pkg
	SV-str	Surface northward wind stress (N/m ²)	ROMS
	SV	Surface northward current velocity (m/s)	ROMS
	SU	Surface eastward current velocity (m/s)	ROMS
	SSH-sd	Standard deviation of SSH (m), at a scale of 0.3-degree resolution	Derived from ROMS
ILD	Isothermal Layer Depth (m). An estimate of mixed layer depth, defined by a 0.5°C deviation from surface temperature	Derived from ROMS	
Landings GAM	SDM-60	Mean monthly probability of presence of sardine (output from SDM) within 60 km of port. Fitted as an interaction term with port	This SDM (see also Muhling et al., 2019)
	Squid	Coast-wide monthly landings of market squid (pounds). Fitted as an interaction term with port	PacFIN landings
	Anchovy	Coast-wide monthly landings of northern anchovy (pounds). Fitted as an interaction term with port	PacFIN landings
	ACL	The current Annual Catch Limit allocation for sardine (mt). A new allocation occurs every 2–8 months	CPS Fisheries Management Plan (pcouncil.org), and Federal Register (federalregister.gov)
	Port	A port factor. Represents port capacity and/or effort, which is assumed constant during the modelled period	Key ports identified from PacFIN landings

Note: Ocean data were taken from the data-assimilative ROMS when fitting the models and estimating the landings simulation goodness-of-fit; ocean data were otherwise taken from the ESM-forced ROMS. The variables in the SDM are listed in order of decreasing relative variable importance in the fitted model (Figure S1).

was sourced from re-analyses developed using multiple ocean colour sensors (Sathyendranath et al., 2019). For projection of habitat suitability, environmental variables were sourced from ROMS simulations of future ocean conditions, forced by output from three ESMs (GFDL-ESM2M, HadGEM2-ES, and IPSL-CM5A-MR), and coupled to the biogeochemical model NEMUCSC (Fiechter et al., 2014, 2018) – an adapted version of the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO; Kishi et al.,

2007). These models are detailed below. SDM predictions were made at the spatial extent of ROMS (30°N to 48°N and offshore to 134°W).

The SDM was fitted to daily data, except for chlorophyll which was monthly (to match the available resolution of NEMUCSC at the time of analysis). Monthly sardine presence (used in the landings model) was the mean of daily values. Covariates and their sources are further detailed in Table 1. Ideally the same chlorophyll product would be used for both model fitting and projection (Table 1), but

NEMUCSC chlorophyll derived from the data-assimilative configuration was not available for entire historical period. However, both chlorophyll products have similar spatial and seasonal patterns and their bias is much less than the spread in projected values between the three ESMs. SST, SSB, and chlorophyll are the most influential variables explaining sardine presence (Figure S1) and model fit is reasonable with AUC = 0.76 (Muhling et al., 2019). Sardine had increased presence at SST between 11 and 16.5°C and at surface chlorophyll >0.3 mg/m³, which agrees closely with the sardine SDM of Zwolinski et al. (2011). The SDM of Kaplan et al. (2016) also showed that SST can be a skilful predictor of sardine distribution. They found sardine associated within slightly warmer waters (14–16°C) and dependent on salinity, although their model was fit to only one year of survey data. Sardine presence increased almost linearly with SSB, indicating that sardine had increased presence at higher abundance, and may relate to the observed increase in sardine occupancy of suitable habitat as stock size increases (Barange et al., 2009).

2.2 | Landings model

A generalized additive model (GAM) was used to model monthly port-level landings as a function of sardine presence from the SDM

and additional covariates (Table 1). We chose a GAM framework here to allow a more explicit evaluation of port-level effects (a BRT can model interaction terms but they are difficult to visualize). Sardine landings for the U.S. West Coast were sourced from the Pacific Fisheries Information Network (PacFIN). We used the 2000–15 period to fit the model, because this period includes the beginning of federal management and allocated ACL for the fishery (2000) to the closure of the fishery due to low sardine biomass (2015). This period also captured the majority of the range in landings and SSB observed since the 1960s, with estimated SSB values >400,000 mt prior to 2011, declining to very low levels in recent years (Barnes et al., 1992; Hill et al., 2018). Sardine were landed at 16+ ports during this period, but most ports were rarely used, so our analysis focused on six main ports: Westport, Ilwaco, Astoria, Moss Landing, Terminal Island and San Pedro. These ports accounted for 95% of landed volume. Based on spatial proximity, we aggregated Astoria and Ilwaco, and San Pedro and Terminal Island, which gave four ports at which we modelled landings (Figure 2). We refer to the two aggregated ports as Astoria and San Pedro. Landings at southern ports are thought to include both southern and northern subpopulations, with perhaps one third of summer landings at San Pedro (5%–15% of coast-wide landings) consisting of the southern subpopulation (Demer & Zwolinski, 2014). Thus, at southern ports our landings model explains landings

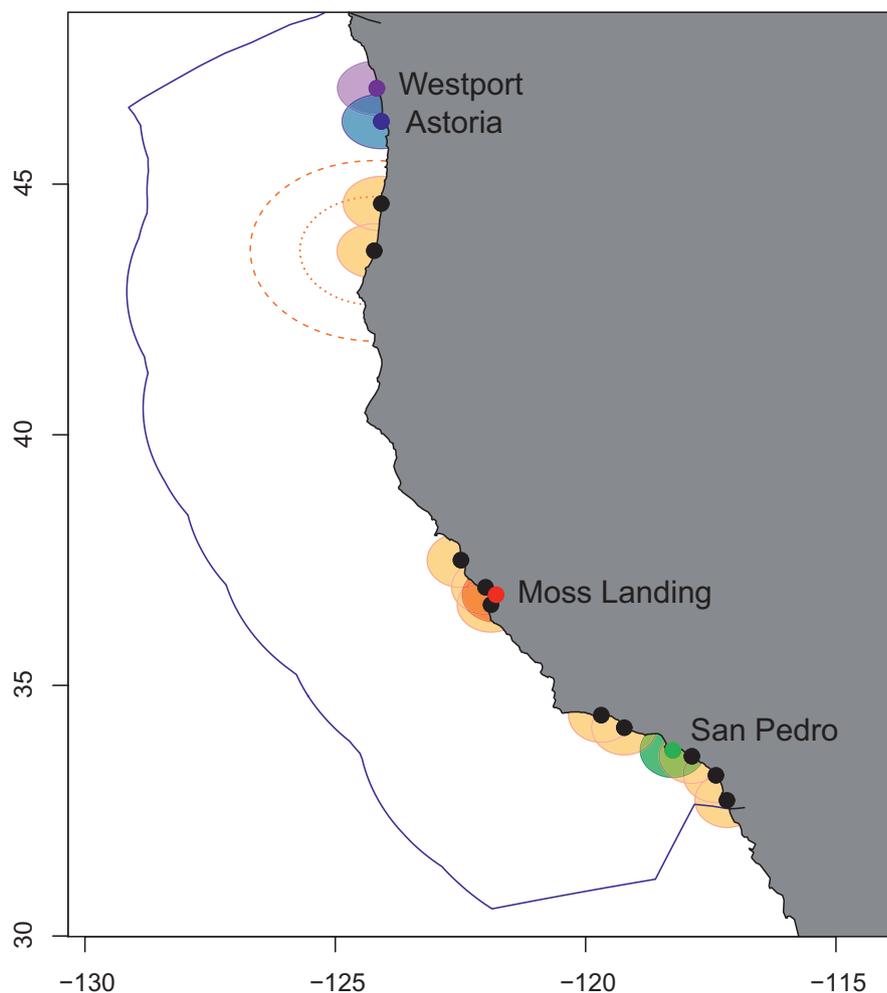


FIGURE 2 Map of the U.S. West Coast and EEZ, and the 14 consolidated ports at which nearly all sardine landings occurred during 2000–15. The four aggregated ports used in our simulation are coloured (Westport, Astoria and Ilwaco, Moss Landing, San Pedro and Terminal Island). The area in which sardine presence was calculated (within 60 km of port, “SDM-60”) is shaded for each port. The area inside 120 and 200 km from port is shown for one northern port (dotted and dashed lines)

of both subpopulations using northern subpopulation habitat suitability, so we expect modelled landings at southern ports to show a weaker response to environmental change and be less accurate than if we could model the change in habitat suitability for each subpopulation separately. Landings could be partitioned into each subpopulation using habitat indices (Demer & Zwolinski, 2014), but this would involve using the SDM twice (once to partition landings, then again to explain the partitioned landings) which could inflate the SDM's accuracy, and would require adjustment of the ACL (which includes both subpopulations). We considered it better to model total landings, but with potentially less accuracy at ports that land both subpopulations.

The northern subpopulation sardine fishery is relatively near-shore, and vessels generally return to port daily to land their catch (Rose et al., 2015). Thus, the probability of sardine presence used in the landings model was the mean monthly probability of presence near each of the four main ports. We evaluated three distances in which to calculate mean sardine presence, 60, 120, and 200 km from port (Figure 2). Model selection showed that the 60 km distance explained the most information for all ports. We term this covariate "SDM-60", which represents the mean monthly probability of presence of sardine with 60 km of a given port.

The sardine fishery has an ACL which is dependent on the estimated coast-wide sardine biomass and allocated 2–3 times per calendar year (Coastal Pelagic Species Fisheries Management Plan, www.pcouncil.org). Until 2005, the allocation was also spatial, with northern and southern areas allocated separate quotas. From 2006 onwards, the allocation was seasonal only, with the ACL allocated across the West Coast region in January, July and September (these changes in allocation were replicated in our simulation). When an allocation is reached, the federal fishery closes until the next allocation. We fitted the landings GAM using only open months, due to negligible landings when the fishery was closed (mean landings in closed months were only 1.8% of mean landings in open months).

Covariates in the landings model included the ACL allocation for that port and period (metric tons), a port-level factor to account for port capacity and effort, and coast-wide monthly landings of two other coastal pelagic species (CPS; northern anchovy *Engraulis mordax*, and market squid *Doryteuthis opalescens*) that showed relationships with sardine landings. We also evaluated monthly fuel price (retail inflation-adjusted diesel price, U.S. Energy Information Administration) as an indicator of fishing costs, and mean monthly price-per-pound deviation for each port as an indicator of fishing value. Sardine price-per-pound data for each landing event were sourced from PacFIN. The deviation metric was used due to the strong relationship between price and landed volume, with price generally declining at higher volumes. We first calculated a supply–demand relationship (a non-linear trend between landed volume and price-per-pound), and the deviation for each landing event was the residual from this supply–demand relationship. Thus, the price-per-pound deviation measured whether a paid price was high or low for that specific landed volume. Model selection was used to find the most parsimonious combination of covariates, evaluated using AIC.

Fuel price was not influential, and price-per-pound deviation complicated prediction of future conditions without contributing much to explained information (+3.5% explained deviance), so both variables were dropped (Table S2). Thus, the final GAM of monthly landings (metric tons) was:

$$\text{Landings} \sim s(\text{SDM60:port}) + s(\text{ACL}) + s(\text{Squid:port}) + s(\text{Anch:port}) + \text{port}$$

where "s" represents a thin-plate regression spline. We included port-level smoothers for anchovy and squid landings and for SDM-60 (Table 1). We found a Tweedie distribution was the most suitable error distribution, as evaluated using residual plots. GAM goodness-of-fit was evaluated using per cent deviance explained, and simulation goodness-of-fit using the correlation and root mean square error of simulated and observed landings for the 2000–15 period. We also evaluated the predictive skill at the seasonal and interannual scales by decomposing both observed and simulated landings into a monthly climatology and anomalies from this climatology, and correlated observed and simulated values for both data sets as well as a 12-month smoothed average of the monthly anomalies.

We assumed that SDM-60 was useful for explaining sardine landings by acting as a surrogate of sardine abundance near port. However, because SDM-60 is highly seasonal, especially at more northern ports, it may also explain landings due to its correlation with other seasonally varying elements of the fishery, such as effort or processing capacity. Thus, we compared the above model with GAMs that included month (as a cyclic cubic regression spline) to evaluate whether a fixed seasonal cycle was better at explaining landings than SDM-60. However, due to collinearity between month and SDM-60, month could not be included in the final model because it created an unrealistic fishery where landings were driven largely by month and very little response to changes in sardine presence. The fit of the GAM including only SDM-60 was comparably good, so we consider the environmental signal meaningful and useful.

2.3 | Simulation and projection of landings

The landings GAM estimated sardine landings in open months only, and a simulation was used to predict in which months the sardine fishery closed (due to exhaustion of an ACL allocation; Figure 1) and how these closures might change in response to changes in sardine spatial distribution. We use "early closure" to refer to this exhaustion of a non-zero ACL allocation and not when an allocation was actually zero (which occurred for the last 6 months of 2015; in which case the simulation assumed landings were always zero).

We simulated landings for 2000–15 using SDM-60 values derived from the data-assimilative ROMS (Figure 1) and compared these to observed landings as a measure of the simulation's goodness-of-fit. For projections, SDM-60 values were derived from ESM-forced ROMS and NEMUCSC. In our simulation, only the ocean conditions were projected, and the values for all other covariates in the landings model (i.e., anchovy and squid landings, ACL allocations) were

identical to those in the 2000–15 reference period. Sardine SSB values used to calculate SDM-60 were also taken from this reference period. We considered it essential to structure our simulation around a reference period because a fishery is a complex system of environmental and human factors that are very challenging to project. In other words, our simulation explored how landings from the 2000–15 reference period might vary due to change *only* in habitat suitability, while maintaining realistic constraints on landings from recent sardine biomass and fishery conditions. We selected 2000–15 as our reference period because (as for model fitting) this period encompasses the start of federal management (and ACL allocation) to fishery closure and was considered a period of representative management and sardine abundance relevant for interpreting projected changes in sardine distribution.

This approach meant that landings were simulated as 16-year time series (the duration of the reference period), using conditions identical to 2000–15 except for the ocean conditions and thus habitat suitability. For example, our simulation could compare port-level monthly landings in 2000–15 with those in 2050–65, with both periods sharing the same SSB, ACL allocation, and anchovy and squid landings, but differing in habitat suitability (i.e., the predicted SDM-60). In order to measure change in landings at an annual time step, we “replayed” the reference period across a 16-year moving window starting every year from 1985, that is simulating 1985–2000, then 1986–2001, and so on each year, until the moving window reached 2080–95. This ensured that every month of the simulation (between 2000 and 2080: the years represented in 16 time series) had 16 values, representing the potential landings given the projected environmental conditions of that year and all possible SSB and ACL values from the reference period.

We used three main metrics to explore impact of changing habitat suitability on northern subpopulation sardine landings: the slope of the linear trend (mt/y) and relative change (%) in projected landings; the seasonality of landings; and the frequency of early closure of the sardine fishery. The linear trend was calculated using linear and quantile regression for the 2000–2080 period, with $p < .005$ indicating a statistically clear trend, and p -values between .005 and .05 providing “suggestive evidence” of a linear trend (Benjamin et al., 2018). The seasonality of landings was measured as the proportion of annual landings occurring in each month. Frequency of early closure of the fishery was measured as the proportion of months in a 16-year times series that were closed due to exhaustion of a non-zero ACL allocation. The choice of reference period, especially the SSB values in that period, determines the absolute magnitude of simulated landings, and influences their absolute rate of change (mt/y) and early closure frequencies. Thus, the actual landings estimated in our projection are only relevant to future periods with sardine biomass within that observed in the 2000–15 period. The relative change in landings (%), however, is more robust to the choice of reference period. This was evaluated using an altered reference period, in which we reordered the SSB and ACL values from 2000 to 15 (we reordered the existing reference period to ensure we stayed within the range of values fitted in the SDM and landings model).

This method removed the very low sardine biomass values, altered the projected SDM-60 values (due to the influence of SSB in the SDM), and created novel combinations of covariate values in the landings model (Figure S8). We are confident our analysis provides a robust estimate of the relative impact that sardine habitat change will have on future landings, whatever those future landings may be. Of course, the more that sardine abundance or the management process change relative to that observed in 2000–15, the less accurate our projections may become. The model fitting and simulation were done in R (R Core Team 2020), relying on packages “mgcv” (Wood, 2017), “gbm” (Greenwell et al., 2019), “dismo” (Hijmans et al., 2017) and “quantreg” (Koenker, 2019).

2.4 | ROMS, ESMs and NEMUCSC

Environmental data were obtained from a CCS configuration of ROMS. This configuration covers 30–48°N and offshore to 134°W, with 0.1 degree (7–11 km) horizontal resolution and 42 terrain-following vertical levels (Veneziani et al., 2009). For the historical period, the model assimilates available satellite and in situ observations of temperature, salinity, and sea surface height (Moore et al., 2013; Neveu et al., 2016). This model has been used extensively to understand and predict distribution shifts for a range of marine species, including Pacific Sardine, off the U.S. west coast (Brodie et al., 2018; Muhling et al., 2019; Smith et al., 2020). For future projections of ocean conditions, the CCS ROMS model was forced by output for 1980–2100 from three global ESMs: GFDL-ESM2M, HadGEM2-ES, and IPSL-CM5A-MR. These three models were chosen to span the range of potential future physical and biogeochemical conditions in the CCS; in terms of temperature change GFDL-ESM2M is on the low end of the CMIP5 ensemble (~2°C by end of 21st century), while warming in HadGEM2-ES is at the upper end of all models (~4°C) and IPSL-CM5A-MR is in between. Similarly, GFDL-ESM2M and IPSL-CM5A-MR project modest increases in primary production for the CCS, while HadGEM2-ES projects a sharp decline. In all cases, we use output from the RCP8.5 scenario. To correct for biases in the ESM output, a “time-varying delta” method is applied before performing the downscaling with ROMS (Poza Buil et al. accepted). For each ESM, changes for the period 1980–2100 are calculated relative to the 1980–2010 climatology. Those ESM changes are then added to the observed 1980–2010 climatology, obtained from atmosphere and ocean reanalysis, to create the bias corrected ROMS forcing. Relative to a “fixed delta” method (Shin & Alexander, 2020), which compares a future period to a historical one, the time-varying delta method has advantages of resolving the full transient response from 1980 to 2100 and capturing the interannual variability from the ESM projection.

To project regional biogeochemical change, we ran ROMS coupled to the biogeochemical model NEMUCSC. NEMUCSC consists of three limiting macronutrients, two phytoplankton size-classes, three zooplankton size-classes, and three detritus pools. NEMUCSC also includes carbon and oxygen cycling based on the formulations of Hauri et al. (2013) and Fennel et al. (2008) respectively (Fiechter

et al., 2014). NEMUCSC was coupled offline to the ROMS down-scaled projection following the approach in Fiechter et al. (2018).

3 | RESULTS

3.1 | Landings model

In the landings GAM, SDM-60 and port were the most influential variables, with squid and anchovy landings somewhat important for northern ports (Figure 3, Table S1, S2). The explained deviance of the GAM was 54% (this decreased to 47% and 40% when using the 120 and 200 km distance versions of the SDM variable,

respectively). ACL allocation was not influential, suggesting that monthly landings generally depended on whether the fishery was open or closed, rather than the size of the quota. There was reasonable to good agreement between observed and simulated monthly landings, with correlations ranging from 0.49 to 0.74 among ports, and 0.7 for total landings (Figure 4 and Figure S2, Table S3). The Mean Absolute Scaled Error between simulated and observed total landings was 0.72, and because this is <1 indicates that the simulated time series is considerably better than a naive “t - 1” forecast (Hyndman & Koehler, 2006). The observed seasonality of landings at Moss Landing, and to a lesser extent San Pedro, was modelled less accurately due to the reduced influence of SDM-60 at these ports. Month was generally no better at predicting landings than SDM-60,

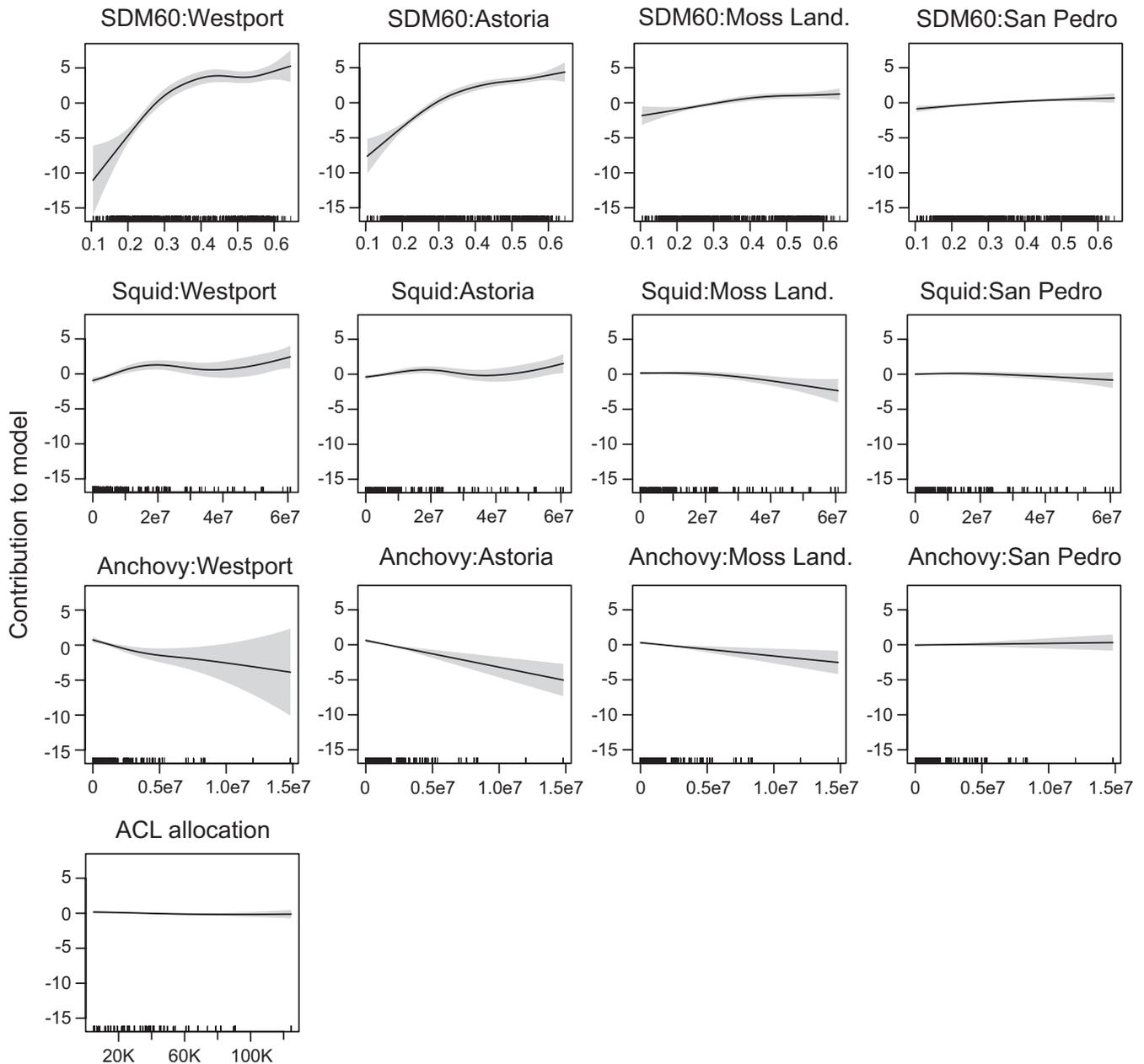


FIGURE 3 Partial effects from the GAM landings model. Standard error is shaded grey. See Table 1 for description of covariates and their units. See Table S1 for parameter estimates and statistical significance

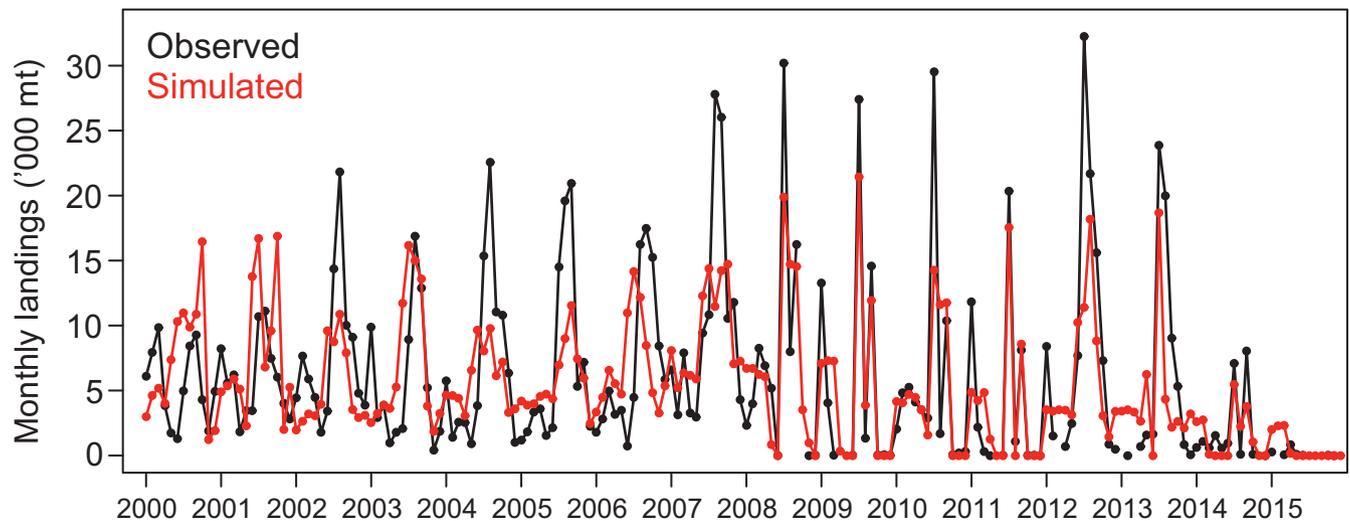


FIGURE 4 Time series of observed (black) and simulated (red) monthly sardine landings (thousands of metric tonnes) for the historical reference period, summed across the four main ports. Thirteen months of low observed landings are not plotted, as these landings were made by fewer than three vessels and are considered confidential data (10/2008, 04/09, 05/09, 05/11, 03/12, 01/13, 03/13, 11/14, 02/15, 07/15, 08/15, 09/15, 12/15). The RMSE between these observed and simulated data was 4886 (Table S3)

and for Westport was considerably worse, and model fit was not greatly improved by including both month and SDM-60 (Table S3), indicating that there are factors other than sardine presence or a fixed fishing season that influence landings at these ports. The stronger relationship between northern subpopulation sardine habitat and landings for northern ports agrees with previous research (Zwolinski et al., 2011). Most ports had high predictive skill of the monthly climatology of landings ($r > .9$), but was considerably lower at Moss Landing (Table S4, Figure S2). There was additional skill at all ports for predicting landing anomalies at both the month and annual scale ($r = .4-.7$; Table S4), but with Astoria showing the least predictive skill due to a 1–2 month mismatch in the timing or duration of the simulated and observed fishing season pre 2007.

3.2 | Projection of habitat suitability and landings

Suitable habitat of the northern subpopulation was projected to change considerably over the coming decades (Figures 5 and S3). Generally, northern waters became more suitable, although the strength of change differed among months and ESMs. HadGEM2 showed the strongest warming and greatest reduction in suitable habitat. The mean monthly sardine presence near port (SDM-60) declined most strongly at southern ports under HadGEM2, and increased most strongly for northern ports under IPSL (Figure S4). The most influential covariates in the SDM were SST and chlorophyll (Figure S1), and the projected monthly means of these variables near the main ports indicates that SST was the more important driver of changes in sardine distribution (Figure S5). Based on the partial effects in the SDM, SST values became more favourable (within 12–16°C) at northern ports, but increasingly warmer than favourable at the more southern ports. Mean chlorophyll was typically within a

favourable range, except at San Pedro which decreased during projection to lower than favourable values (Figure S5).

Projected change in SDM-60 caused landings to generally increase at northern ports (Westport and Astoria) and decrease at the southern ports (Moss Landing and San Pedro) (Figures 6 and 7). This result was generally robust across all ESMs, except for HadGEM2 which indicated no change in landings at Astoria (due partly to differences in the port-level effects from anchovy and squid). The mean linear rate of change in landings from 2000 to 2080 ranged from a decrease of 104 mt/y at San Pedro (IPSL) to an increase of 212 mt/y at Astoria (IPSL) (Table 2). Projected total landings (the sum of port-level landings) differed considerably among ESMs, with IPSL indicating an increase of 115 mt/y, HadGEM2 a decrease of 171 mt/y, and GFDL a strong increase through 2050 then decrease (Figure 7) resulting in a statistically unclear linear trend. Quantile regression quantified rate of change for years in which landings were high (the 0.75 quantile) or low (0.25 quantile). Landings in low years generally increased or decreased more slowly, and landings in high years did so more quickly (Table 2, Figures 6 and S6,S7). This meant that ports with projected increases in landings had increased inter-annual variation in landings (and the opposite for ports with projected decreases). All ports still experienced years with comparably low landings because the reference period contained years with low sardine biomass and thus low ACL. The projected absolute rates of change in landings (mt/y; Figure 6) are influenced by magnitude of SSB in the reference period, while the relative change (%; Figure 7) is more robust and likely indicative of change for a broad range of possible sardine trajectories (Figures S8,S9).

The timing of the fishing season often changed by the end of the simulation period, due to change in the seasonality of the suitable habitat near port (Figure 8). Under HadGEM2, the fishing season appeared to become longer, due to more equal habitat suitability

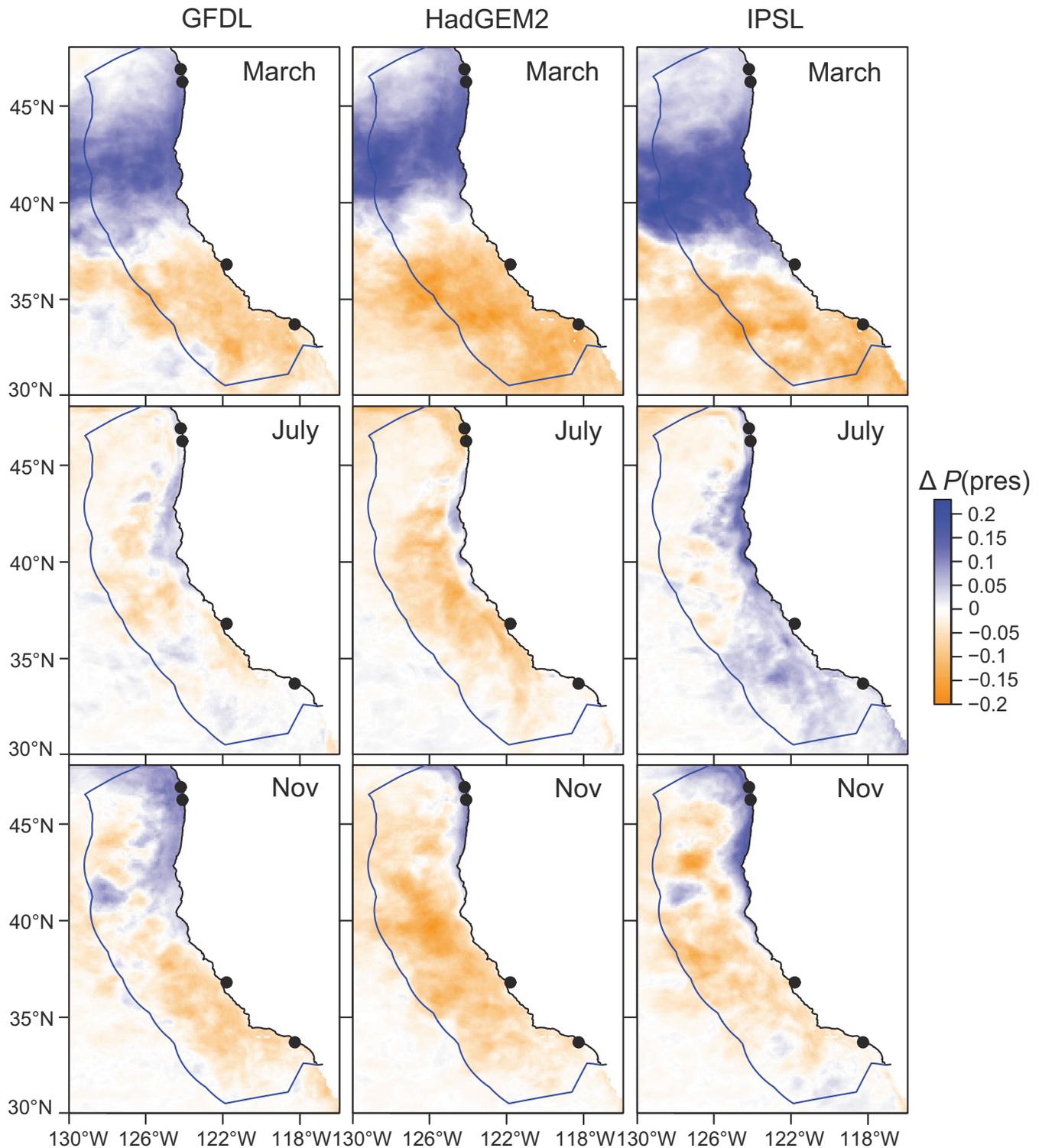


FIGURE 5 Mean change in projected sardine habitat suitability (2040–55 period minus 2000–2015 period), in the three ESMs in three representative months. Blue indicates an increase in habitat suitability, and orange a decrease, over this ~40-year period. The four main ports are indicated (black dots). Units of change represent probability of sardine presence. An end of century comparison is illustrated in Figure S3

throughout the year. Under IPSL, landings expanded into the early part of the year, but generally became more focused in fewer months in the later part of the year, which was due to increased landings in some months and more frequent closure of the fishery due to an

ACL allocation being reached. The fishing season changed the least under GFDL. Increased landings resulted in more frequent early closures. Under IPSL, which showed the largest increase in total landings (Figure 7), early closure of the fishery increased in frequency,

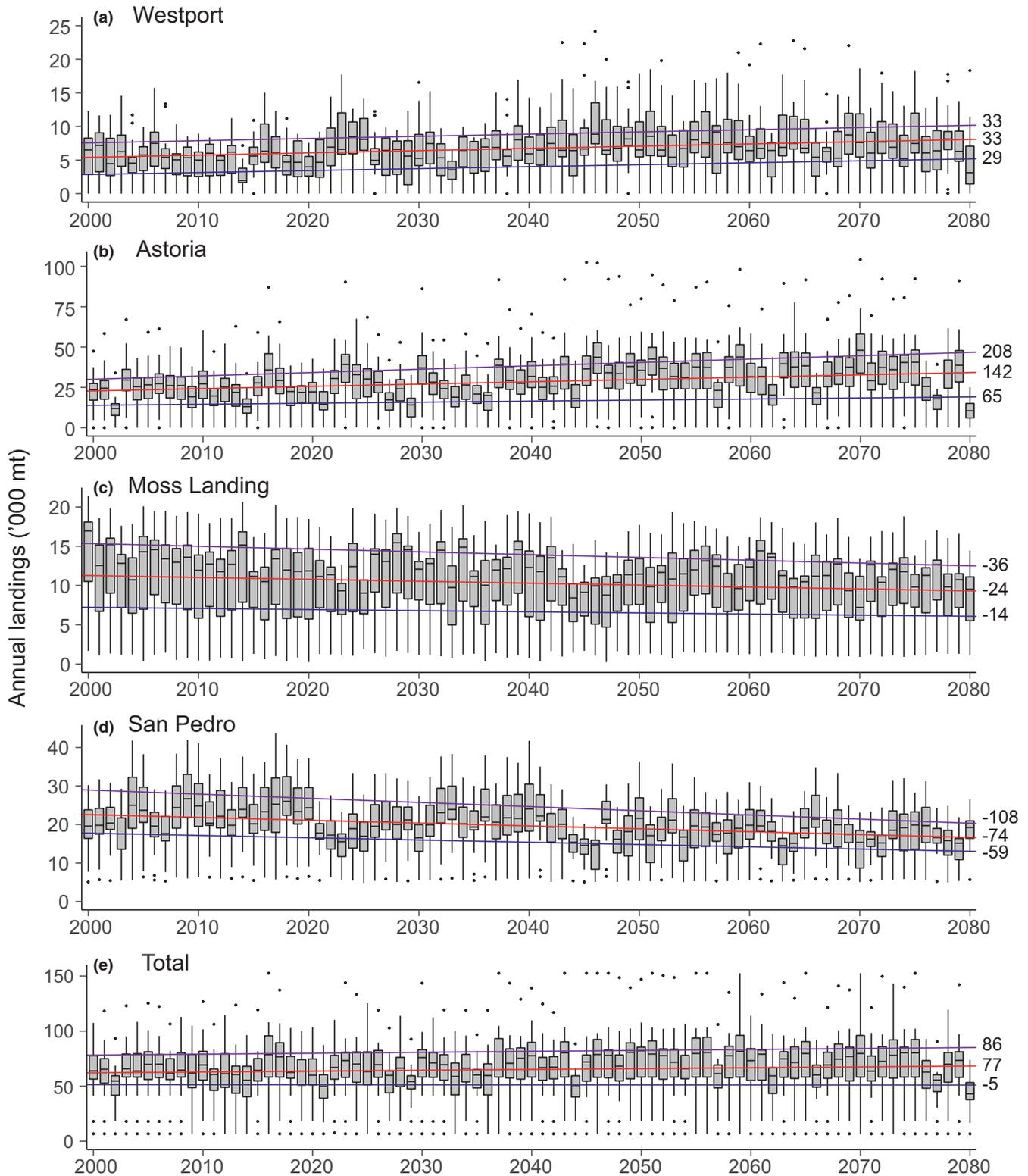


FIGURE 6 Time series of port-level and total simulated sardine landings from 2000 to 2080, given change in habitat suitability as predicted by ROMS forced by GFDL-ESM2 M. Each boxplot contains 16 data points, representing each position in the 2000–15 reference time series. Thus, these boxplots represent the likely interval of annual landings given each year's environmental conditions, and 2000–15 sardine biomass and management conditions. The lines are fitted linear (red) and quantile regression (purple and blue), and the slopes are reported on the right; for example, mean landings at San Pedro decreased by 74 mt/y (red line), while landings in the best years (0.75 quantile, purple) decreased faster at 108 mt/y, and landings in the worst years (0.25 quantile, blue) decreased at 59 mt/y. See Table 2 for a summary of regression slopes for each ESM. See Figures S6,S7 for the two other ESMs

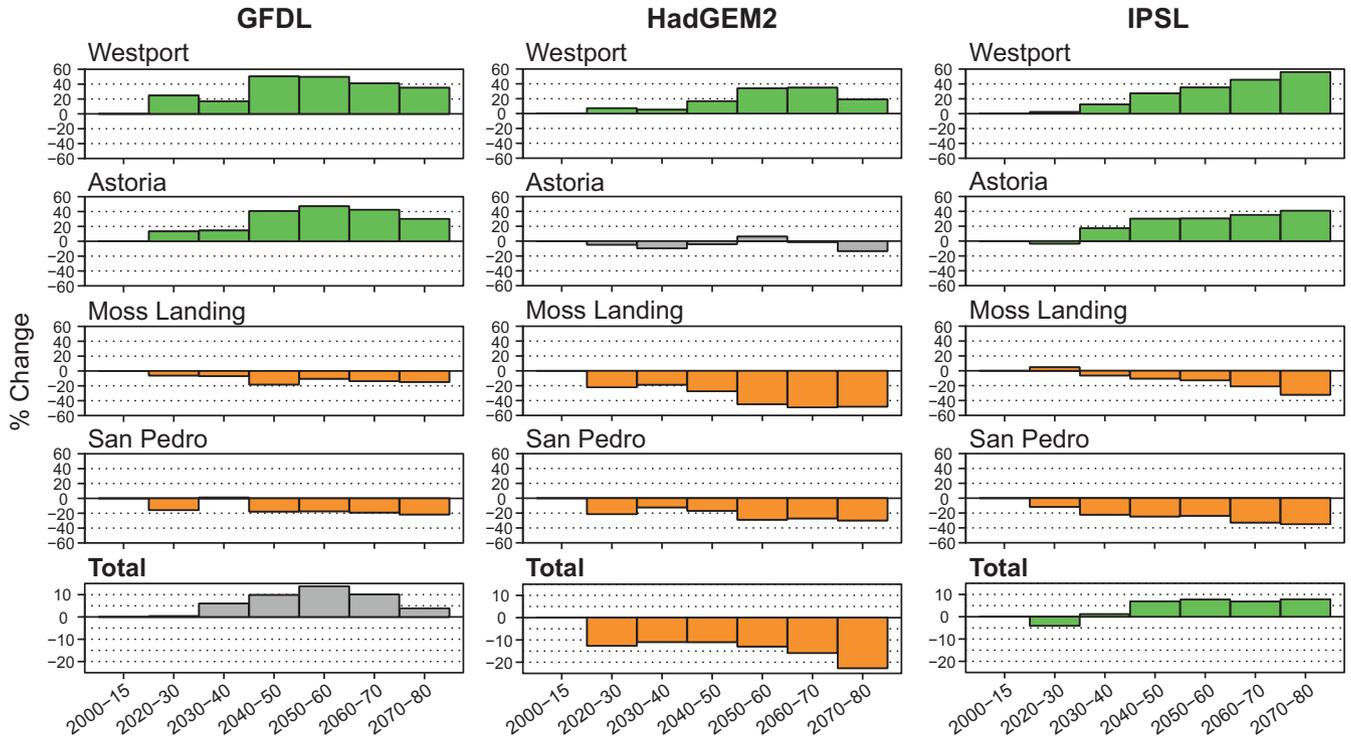


FIGURE 7 Summary of per cent change in mean landings (due to change in sardine distribution only) for future decades relative to the 2000–15 period, for each ES. The 2000–15 period was also derived from the ES-forced ROMS (i.e., not observed or data-assimilative ROMS). Colours indicate statistically clear ($p < .005$) linear trends over the 2000–80 period (green = increase, orange = decrease), as reported in Table 2 and illustrated in Figure 6 and Figure S6,S7. Grey bars indicate trends that were not statistically clear. This rate of change result is reasonably robust to reference period values (Figure S9)

Port	ES	Mean	0.25	0.75
Westport	GFDL	33 (<.001)	29 (<.001)	33 (<.001)
	HadGEM2	25 (<.001)	-2 (.781)	31 (<.001)
	IPSL	57 (<.001)	38 (<.001)	84 (<.001)
Astoria	GFDL	142 (<.001)	65 (.011)	208 (<.001)
	HadGEM2	-19 (.282)	-62 (.063)	22 (.315)
	IPSL	212 (<.001)	167 (<.001)	239 (<.001)
Moss Landing	GFDL	-24 (<.001)	-14 (.149)	-36 (<.001)
	HadGEM2	-87 (<.001)	-54 (<.001)	-117 (<.001)
	IPSL	-50 (<.001)	-46 (<.001)	-51 (<.001)
San Pedro	GFDL	-74 (<.001)	-59 (<.001)	-108 (<.001)
	HadGEM2	-90 (<.001)	-55 (<.001)	-130 (<.001)
	IPSL	-104 (<.001)	-152 (<.001)	-98 (<.001)
Total	GFDL	77 (.026)	-5 (.943)	86 (.007)
	HadGEM2	-171 (<.001)	-219 (<.001)	-210 (<.001)
	IPSL	115 (.003)	0 (.999)	167 (<.001)

TABLE 2 Results of linear (mean) and quantile (0.25, 0.75) regression exploring the linear trends in landings (as in Figure 6)

Note: Reported are the slope (mt/y) and p -value (in parentheses). Statistically clear linear trends are highlighted grey ($p < .005$).

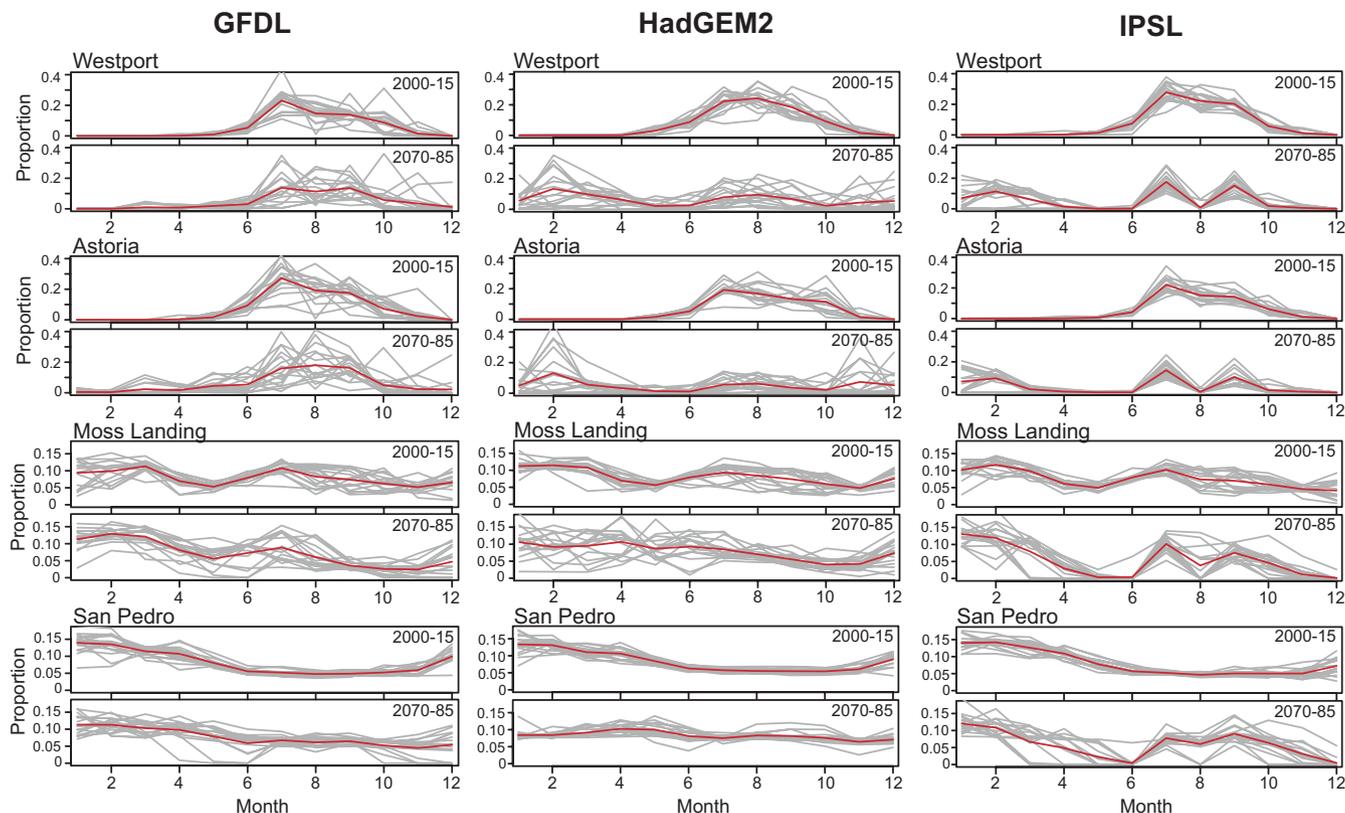


FIGURE 8 Change in fishing seasons between two periods (2000–15 and 2065–80) for each port and ESM. Shown is the proportion of landings in each month for each year in the given period (grey lines), calculated as the median of the 16 replicates of that year from the 2000–80 simulation. The mean of those 16 medians is also shown (red line)

exceeding 40% of months by 2070 (Figure S10). Under HadGEM2, early closure of the fishery occurred in ~10% of months by 2070.

4 | DISCUSSION

Our projection of the suitable habitat of the northern subpopulation of Pacific sardine in the CCS showed a northward distribution shift over the coming decades, resulting in a decrease in U.S. landings at more southern ports and an increase at northern ports. This result was robust across the three ESMs. The impact on total landings was not consistent across climate projections, with the impact of a shifting sardine distribution on total landings ranged from a 15% increase by 2055 to a 20% decrease by 2070. This variation was due to differences in ocean conditions projected by the three ESMs and how these differences interacted with the modelled port-level responses to habitat suitability. The three projections also differed in their estimated impacts on the fishing season, which ranged from little change to the season (GFDL), an extension in season length (HadGEM2), to contraction driven by more frequent early closures (IPSL).

Climate projections have indicated a global redistribution of catch potential (Cheung et al., 2010) and fish production this century (Barange et al., 2014), which may have a large impact on fishing revenues due to changes in fishing areas and catch composition

(Lam et al., 2016). Redistribution of species will also reduce fishing opportunities, unless fishing communities and management agencies show considerable adaptation (Rogers et al., 2019). For the U.S. West Coast, Morley et al. (2018) projected a large distribution shift for Pacific sardine, which was one of their “low uncertainty” species. Our simulation supports this large shift and builds on these studies by quantifying the relative impact of this shift on port-level landings, and identifying locations that may have increased, or decreased, opportunities.

The landings GAM showed a strong association between sardine probability of presence and landings, but this was stronger at the northern ports. Given that the use of the northern habitat can be highly seasonal and related to sardine SSB, it is not surprising that landings in this area correlate more with predicted sardine presence. At the more southern ports, there were other important factors influencing landings that we could not identify, which might include the presence and landings of the southern sardine subpopulation whose habitat suitability we did not estimate (discussed below). Although the correlations between observed and predicted landings were less strong at these ports, the magnitude of the interannual impact of sardine distribution was robust (Figures 6 and 7). The landings of northern anchovy and market squid were also found to correlate with sardine landings, and again this was stronger for the two northern ports. These relationships indicate that the ability of the fishery to take advantage of a shift

in habitat depends considerably on the distribution and abundance of other CPS. This provides support for further management consolidation of CPS species, and for the idea that exposure of fishing communities to risk from distribution shifts is strongly influenced by the portfolio of species caught (Rogers et al., 2019) and their spatial and temporal availability.

Quantifying change in the seasonality of the fishing season, and the frequency of early closures, indicate the potential constraints of a seasonal ACL allocation scheme. Under HadGEM2 and IPSL, the beginning of the calendar year became more important for landings at northern ports, which contributed to the early closure of the fishery by June under IPSL (Figure 8). Closures were then soon apparent again in August under IPSL. It seems unlikely that the same January, July, and September ACL allocation scheme used during most of the reference period allowed the flexibility required to fully adapt to the changing seasonality of the sardine distribution. Further research could focus on the ability of the fleet to shift effort between months (and do so safely), given additional constraints such as weather.

4.1 | Simulation challenges and developments

We stress again that our simulation does not attempt to forecast actual sardine landings. Landings are the result of a complex interplay of biological, ecosystem, management, and socioeconomic factors. Instead, our analysis isolates one important signal – that of climate-driven spatial distribution changes – while maintaining realistic “reference” values for all other factors. Thus, our results are best interpreted by examining relative change in landings and using this to infer how the single stressor of spatial distribution change may compound other “stressors” influencing the future sardine fishery. Our use of a reference period allowed us to explore long-term projection of climate change impacts on landings, which would otherwise be very challenging to achieve, especially if modelling sardine population dynamics.

The key challenges of our correlative framework fall under three areas: (1) model uncertainty, (2) assumptions of SDMs and correlative models, and (3) unexplored dynamics of sardine distributions. In terms of model uncertainty, we focused on the uncertainty in the projection of ocean conditions (by using three ESMs) and on the uncertainty associated with fishery conditions in the reference period, and replaying the reference period allowed us to measure the “effect size” of change in landings relative to the 2000–15 variation in CPS abundance and ACL allocation (Figure 6). Additional sources of uncertainty are primarily the unexplained variation in the SDM and landings GAM, and uncertainty in future emissions (i.e., RCP scenario). Propagating these additional sources of uncertainty to the results could be done by repeating the analysis with other RCP scenarios, other plausible SDMs (although Muhling et al., 2020 found similar model fits across BRT, GAM, and random forest models), and by repeating the simulation using the predicted standard error (or values sampled from the posterior distributions) from the landings GAM. The computational burden of our simulation was already

high, so a priority for subsequent projections would be developing an approach to incorporate additional uncertainty efficiently. There may also be potential to identify uncertainty more efficiently by integrating the occurrence and landings models using a state-space or hierarchical framework, depending on the source and temporal resolution of the data.

Correlative SDMs are often used for projecting spatial distributions, and appear well suited for modelling the distribution of Pacific sardine (Morley et al., 2018; Muhling et al., 2019; Zwolinski et al., 2011), but these models also require careful interpretation. A typical assumption of SDMs is the stationarity of the fitted habitat associations, which in our case meant assuming the habitat preferences of sardine were constant for the entire simulation. Although marine species often track climate velocities (Pinsky et al., 2013), which indicates conservation of the thermal niche, acclimation is also possible. Pacific sardine as a species can tolerate a broad range of temperatures and can be considered a warm-affinity species (Cheung et al., 2015), so there may be potential for this northern subpopulation to acclimate. The potential for non-stationarity may be most relevant to rapid habitat change, and sardine habitat suitability can lose some accuracy for explaining spatial distribution under anomalous heat-wave conditions (Muhling et al., 2020). A useful area of research, then, would be SDMs that also incorporate regional (Thorson, 2019) or geographic factors that might constrain the rate at which species track their dynamic environment. Also, we found that “month” had similar predictive skill as “SDM-60” for predicting landings, and it was clear that neither could explain all the observed seasonality of landings (Table S3). We did not include month in our landings model, because it creates a fishery largely unresponsive to the sardine presence or SSB, but this result indicates that there may be unidentified factors influencing the seasonality of sardine landings which could further constrain projected changes to landings. These factors may include the presence and landings of the southern subpopulation (Demer & Zwolinski, 2014), weather constraints to fisher access, as well as socioeconomic factors and regional environmental forcing not included in our SDM (Martínez-Rincón et al., 2019). Future evaluation of a longer time series of landings, and careful evaluation of known drivers of landings, are essential for ensuring correlative models such as this contain useful information and are interpreted correctly. Another consideration is that, by including a “port” factor in our landings GAM, we assumed that these ports would remain as influential (in terms of port capacity and effort) as they were in the 2000–15 period. A fishery will have some flexibility to respond to a changing target species distribution, so our projection estimates the impact on landings given very little change in the fishery (other than some flexibility in shifting effort among months). And finally, as a result of the sometimes patchy trawl survey used to build the SDM, and the nature of BRTs, the modelled effect of temperatures <11 and >17°C were constant (Figure S1), meaning that we lacked skill in resolving changes in habitat suitability at the more extreme temperatures. Thus, SDM-based projections would benefit from observations sampled across a broader range of environmental conditions, or additional “hybrid” information on a species' temperature

preferences and physiological limits. This hybrid information might include the aerobic limitation of habitat, which has shown to play a key role in the coastal distributions of other CPS in the California Current (Howard et al., 2020).

In terms of unmodelled dynamics of sardine, a key challenge in the CCS is accounting for the northern and southern sardine subpopulations. Our study simulated the habitat suitability of only the northern subpopulation, due to the coverage of the trawl survey, and used this to explain total landings. The southern subpopulation, predominantly in Mexican waters, also migrates north and can contribute to landings in Southern California (Demer & Zwolinski, 2014). Thus, our simulation was less successful at explaining landings at southern ports and unable to distinguish the different trajectories of habitat change for the two subpopulations. If the southern subpopulation also shifts north and contributes more to future catches at the southern ports, then our analysis overestimates the decline in Southern California landings, although projection of the suitable habitat of the southern subpopulation indicates only a subtle poleward range shift (Petatán-Ramírez et al., 2019). The potential for landings of the southern subpopulation at southern ports, and the uncertainty of these landings in our simulation, highlights the value of continued monitoring of the distribution and landings of the southern subpopulation, and the value of integrating spatially explicit models of both subpopulations.

Other potential developments of this framework relate to multi-species projection and scenario testing (such as alternative management strategies). Our simulation uses the reference period to specify anchovy and squid landings, but these too could be influenced by the environment. Given the likely importance of landings of multiple CPS to fishery resilience, a useful development could be a joint modelling framework predicting landings of numerous CPS (e.g., sardine, anchovy and squid) as a function of each species' habitat suitability. It would be important in such a framework to account for the covariance of these landings based on processes such as price or demand, to represent preferential targeting of a species when they are equally present. In our simulation, this was accounted for by squid and anchovy smoothers with their landings specified by the reference period, but when each species is a response variable this would require a different approach. Another valuable development may be using statistical representations of a fishery for exploring its sensitivity to hypothetical changes; and when these changes are a management strategy, such scenario testing would be useful to identify strategies most robust to sardine distribution shifts which could then be targeted for tactical management strategy evaluation. In a purely hypothetical example, we compared the impact of a shifting sardine distribution on landings given an observed ACL (Figure 7) to a hypothetical period where every ACL allocation was reduced by 50%. This resulted in the same general patterns, but with reduced landings at northern ports (Figure S11). Because halving the ACL had a disproportionately large impact on northern ports, the total landings of the fishery did not respond as positively to a northward shift in sardine habitat. Halving the ACL also increased the frequency of

early closure of the fishery, and was a proportionally stronger constraint to the duration of the fishing season. Caution must be applied when using our correlative framework for this type of scenario testing, because sardine SSB is specified not modelled. For example, simulating a greatly increased ACL may not be insightful, because the simulation may project sustained large landed volumes of sardine which become increasingly unlikely due to the lack of feedback between landings and SSB. Scenarios that are less likely to cause change to the population dynamics of sardine may be the most suitable for this approach, such as a seasonal allocation strategy for a specified ACL.

5 | CONCLUSIONS AND MANAGEMENT IMPLICATIONS

If the northern subpopulation of sardine maintains its habitat preferences, especially its thermal niche, their distribution will likely shift northwards and they will be encountered and landed more frequently in northern U.S. West Coast waters. The impact of this distribution shift on landings may be large at some ports (e.g., a 30%–50% decline by 2080), but less severe overall, due to increased landings in the northern CCS counteracting decreased landings in the southern CCS. If the fishery has flexibility to shift effort and port capacity, then these impacts could be reduced further, although considerable impact could still occur at the port and fisher level.

Some implications of the study for management are as follows: (1) the likely value of maintaining capacity for Pacific sardine at northern ports, and exploring additional opportunities to land sardine in northern California (Figure 5); (2) the increasing value of periodic evaluation of the seasonal ACL allocation due to its potential to constrain landings in a shifting fishing season; (3) the importance of considering the futures of species shared in a portfolio, in this case CPS, as we found the timing of other CPS landings constrained sardine landings even when sardine presence was high; (4) the value of continued evaluation of the distribution of the southern subpopulation in U.S. West Coast waters; and (5) the value of incorporating possible futures from multiple climate models to identify which projected impacts are robust and which uncertain, especially when a species has a relatively narrow preferred-temperature niche.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

All authors conceived the study. JAS, DT, BM and JS designed the analysis. JAS and BM performed the analysis. MPB, JF and MGJ performed the ocean projections. JAS wrote the first draft of the manuscript, and all authors revised it.

DATA AVAILABILITY STATEMENT

Historical ROMS re-analyses are available from oceanmodeling.ucsc.edu. Contact authors for ROMS and NEMUCSC projections. Commercial catch data were accessed through the PacFIN (pacfin.psmfc.org), but are confidential data and cannot be made public. Contact authors for R code to run the SDM and simulation.

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SUPPORTING INFORMATION

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

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