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Projecting species distributions using fishery-dependent data

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Abstract

Many marine species are shifting their distributions in response to changing ocean conditions, posing significant challenges and risks for fisheries management. Species distribution models (SDMs) are used to project future species distributions in the face of a changing climate. Information to fit SDMs generally comes from two main sources: fishery-independent (scientific surveys) and fishery-dependent (commercial catch) data. A concern with fishery-dependent data is that fishing locations are not independent of the underlying species abundance, potentially biasing predictions of species distributions. However, resources for fishery-independent surveys are increasingly limited; therefore, it is critical we understand the strengths and limitations of SDMs developed from fishery-dependent data. We used a simulation approach to evaluate the potential for fishery-dependent data to inform SDMs and abundance estimates and quantify the bias resulting from different fishery-dependent sampling scenarios in the California Current System (CCS). We then evaluated the ability of the SDMs to project changes in the spatial distribution of species over time and compare the time scale over which model performance degrades between the different sampling scenarios and as a function of climate bias and novelty. Our results show that data generated from fishery-dependent sampling can still result in SDMs with high predictive skill several decades into the future, given specific forms of preferential sampling which result in low climate bias and novelty. Therefore, fishery-dependent

data may be able to supplement information from surveys that are reduced or eliminated for budgetary reasons to project species distributions into the future.

1 | INTRODUCTION

The world's climate is changing at an unprecedented rate. Over the last century, global average temperature has increased by 0.85°C, resulting in biological responses across terrestrial, freshwater and marine environments (Cheung et al., 2015; Morley et al., 2018; Nye et al., 2009; Pecl et al., 2017). Species may respond to a changing climate in a variety of ways, including acclimatizing, adapting, moving to an area with a more suitable environment or even dying. The responses of species to climate change, such as the rate of change in distributions, are more pronounced in the ocean, which absorbs the majority of the excess atmospheric heat from greenhouse gas emissions (Pinsky et al., 2019; Poloczanska et al., 2013, 2016; Sorte et al., 2010). Changes in species distributions pose significant challenges and risks to resource management and the communities and economies that depend on marine resources (Pinsky et al., 2019). This is particularly so for fisheries that are faced with species shifting outside of historical fishing areas or across management boundaries (Ishimura et al., 2013; Sumaila et al., 2020). In light of this, there is an increasing need to predict how marine species distributions will respond to changing conditions. Accurate projections of future species distributions can inform our understanding of potential impacts on fisheries and fishing communities, climate change risk assessments, and sustainable fisheries management that can anticipate, prepare and account for these changes (Rogers et al., 2019; Selden et al., 2019; Smith, Muhling, et al. 2021).

Correlative species distribution models (SDMs) are increasingly being used to project future species distributions to aid management decision making in the face of a changing climate (Cheung et al., 2009; Hazen et al., 2013). SDMs use statistical methods to relate species occurrence or abundance to underlying environmental conditions, and then use those fitted relationships to predict current and future distribution patterns (Elith & Leathwick, 2009; Guisan & Thuiller, 2005). SDMs generally perform better when predicting within the same time and space as the data used for calibration (e.g. interpolation), but performance can decline when projecting into novel environmental conditions and locations (i.e. extrapolation) (Meyer & Pebesma, 2021; Muhling et al., 2020; Sequeira et al., 2018). However, in some cases, SDMs can perform well when predicting abundance and distribution under novel conditions (Becker et al., 2019). As climate change continues to cause novel conditions to emerge (Smith et al., 2022), understanding when models can perform well and what factors impact SDM performance under novel conditions is increasingly important.

An important factor that can affect SDM performance, particularly with regard to their ability to accurately project species distributions far into the future, is quality of the training data used to fit the models. In the case of marine fisheries, occurrence and abundance data mainly come from two sources, fishery-independent and/or fishery-dependent data. Fishery-independent data are often collected through expensive research programmes which conduct standardized scientific surveys over large areas. Fishery-independent data collected via scientifically designed and standardized sampling gear and designs are particularly valuable as these sampling properties facilitate straightforward empirical estimation of population density and abundance. However, due to high cost and logistical challenges, fishery-independent data may not be available

for all species, seasons and regions (Dennis et al., 2015). This is particularly the case for many highly migratory species, which tend to have large and dynamic ranges (Lynch et al., 2018).

Fishery-dependent data often come from scientific observers on commercial fishing vessels, fish tickets (i.e. landing receipts) and/or industry-reported logbooks and are frequently the only distribution data available for many species. They may provide some advantages over fishery-independent data, particularly with respect to the number of observations available. Additionally, fishery-dependent data may actually be preferred in certain circumstances. For example, when the goal is to understand how a species may interact with the fishery (Crear et al., 2021). However, a potential concern with fishery-dependent data is their non-probabilistic, preferential sampling scheme. Economic, social and management factors drive the distribution of fishing locations; for example, fishers actively seek out areas with expected high concentrations of their target species (Pennino et al., 2019), but also may make decisions on where to fish based on local knowledge and experience (St. Martin & Hall-Arber, 2008), management restrictions such as bycatch avoidance, closed areas and landings requirements, as well as economic considerations such as fuel costs influencing the distance they are able or willing to travel from ports (Bucaram et al., 2013; Daw, 2008; Sampson, 1991; Smith & Wilen, 2003; Wilen, 2004).

The locations of fishing activity are therefore not random and not independent of the response variable (e.g. species abundance) (Conn et al., 2017; Diggle et al., 2010; Pennino et al., 2019). Such preferential sampling violates a statistical assumption that sampling locations have been chosen independently of the value expected at a given location and can result in biased predictions of abundance and distribution (Alglave et al., 2022; Conn et al., 2017; Diggle et al., 2010; Pennino et al., 2019; Rufener et al., 2021). Additionally, the non-random nature of fishing locations often results in the fishery-dependent data being spatially clustered relative to the underlying spatiotemporal distribution of the target species, which can result in poor representation within the data of the complete range of environmental conditions present in an area (Kadmon et al., 2004). The quality of an SDM and its ability to provide accurate predictions, particularly under novel conditions, can be strongly affected by such spatially and environmentally biased sampling schemes (Baker et al., 2022; Kadmon et al., 2004; Støa et al., 2018; Yates et al., 2018).

Despite a general understanding of these potential biases and impacts on SDM performance, more work is needed in assessing the relative magnitude of such biases coming from different types of fishery-dependent sampling and understanding the factors that impact the relative magnitude. Several recent studies show that fishery-dependent data does not always result in biased predictions and may still be appropriate to analyse with standard statistical approaches (Ducharme-Barth et al., 2022; Pennino et al., 2016), or can be complementary to fishery-independent data using integrated methods (Alglave et al., 2022; Rufener et al., 2021). Therefore, considering that resources are increasingly limited at agencies for fishery-independent surveys, it is critical we understand the
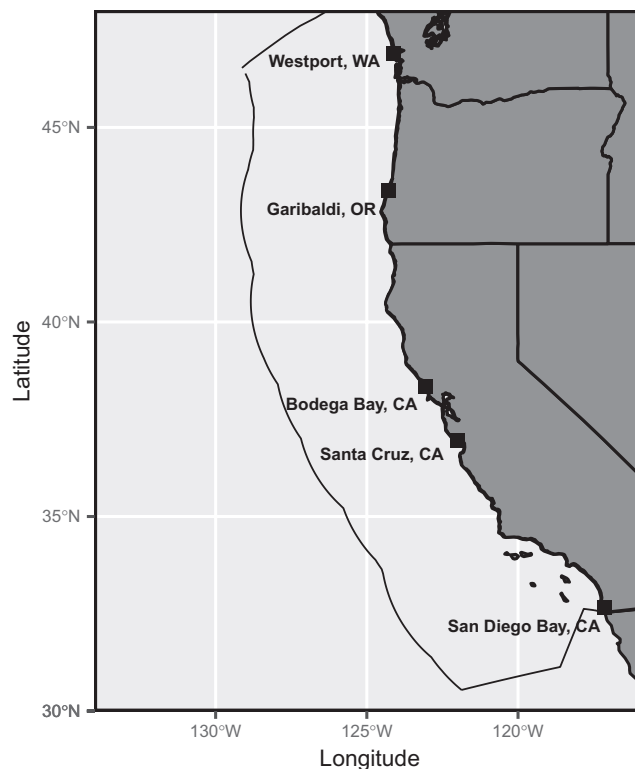
FIGURE 1 Map of the study area, showing the entire ROMS domain. The black outline off the coast of California (CA), Oregon (OR) and Washington (WA) indicates the United States exclusive economic zone (EEZ). The ports used for the distance from port sampling scenarios are labelled and indicated with black squares on the map.

strengths and limitations of SDMs developed for evaluating future fish distributions from fishery-dependent data.

In this study, we explore the potential for fishery-dependent data to inform SDMs and abundance estimates and quantify the bias resulting from different fishery-dependent sampling scenarios in the California Current System (CCS; Figure 1). Specifically, we ask:

1. How do various types of fishery-dependent sampling affect SDM performance, relative to a randomized sampling process?
2. What is the timescale over which future SDM performance degrades, and is it affected by the type of fishery-dependent sampling?

We use a simulation approach to generate the 'true' distribution of a species based on static relationships between abundance and environmental variables. We then simulate a random sampling and several different fishery-dependent sampling processes to collect species observations and fit two types of SDMs (generalized additive models (GAMs) and Boosted Regression Trees (BRTs)) to those data. We then evaluate the ability of the SDMs to project changes in abundance, centre of gravity and spatial patterns of distribution into the future, and compare the time scale over which model performance degrades between the different sampling scenarios and as a function of climate bias and novelty. This simulation approach

is advantageous because it allows us to test the impacts of different sampling scenarios on model performance against a known 'truth', which is not possible with in situ data.

2 | METHODS

2.1 | General framework

To quantify the impact of fishery-dependent sampling bias on the ability of SDMs to predict current and project future species distributions, we used a simulation-estimation process consisting of four main steps (Figure 2): (1) develop an operating model (OM) to simulate a virtual species distribution, (2) sample the virtual species distribution with simulated random and fishery-dependent sampling procedures, (3) use the simulated data (training period 1985–2010) to fit an estimation model (the SDM), and project the SDM from 2011 to 2100 under climate change and (4) evaluate performance of fitted models by comparing the output of SDM predictions against the 'true' simulated observations. Here, we provide an overview of the key aspects of the simulation. More details can be found in the Supplemental Methods and in Table S1, and the Rcode for this simulation can be found on github (https://github.com/Melissa-Karp/Fishery-dependent-SDM-projections).

2.2 | Operating model

We used the *virtualspecies* package (Leroy et al., 2016) in R version 3.6.1 (R Core Team, 2019) to build our operating model. This enables us to not only simulate species-environment responses and convert habitat suitability to presence–absences or abundance but also incorporate biases into the process of sampling occurrences.

2.2.1 | Environmental variables

Environmental data were obtained from a California Current System (CCS) configuration of the Regional Ocean Modeling System (ROMS). This configuration covers 30–48° N and inshore of 134° W, with 0.1 degree (7–11 km) horizontal resolution and 42 terrain-following vertical levels (Pozo Buil et al., 2021; Veneziani et al., 2009). For projections of ocean conditions, the CCS ROMS model was forced by output for 1980–2100 from a global Earth System Model (ESM; HadGEM2-ES) under the RCP8.5 emission scenario. For this study, 1985–2010 was considered the 'historical' period, and 2011–2100 the 'future' period, but both periods were sourced from the same ESM-forced projection. To correct for biases in the ESM used to force ROMS, a 'time-varying delta' method was applied before performing the downscaling with ROMS, in which ESM changes (calculated as departures from the 1980–2010 climatology) were added to the observed 1980–2010 climatology (Pozo Buil et al., 2021; Smith, Muhling, et al. 2021). To project regional biogeochemical change

(including phytoplankton biomass), ROMS is 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). NEMUCSC consists of three limiting macronutrients, two phytoplankton sizeclasses, three zooplankton size-classes and three detritus pools. Following the approach in Fiechter et al. (2018), NEMUCSC was coupled offline to the ROMS downscaled projection (Pozo Buil et al., 2021). Environmental variables of interest were sea surface temperature (SST; C), mixed layer depth (MLD; m), surface chlorophyll-a (Chl-a; mg m-3) and zooplankton integrated over 200 m (zoo_200; mmol N m-2).

We used only one ESM to keep the simulation manageable, and selected HadGEM2-ES because it is at the upper end of projected end-of-century warming for the CMIP5 ensemble (~4°C) and thus maximizes the signal-to-noise ratio. We note that our results may be somewhat specific to the CCS, and that the magnitude of change (and trends in specific variables) projected by HadGEM2-ES can differ considerably to that projected by other ESMs and within other systems (Pozo Buil et al., 2021). However, the directionality of projected change in offshore waters, which are the focus of this study, are consistent across three ESMs examined in Pozo Buil et al. (2021).

2.2.2 | Generating the species distribution and abundance

We based the simulated species on a pelagic predator which responds to sea-surface temperature (SST), prey fields and mixed layer depth (MLD) in the CCS and is present during spring. We chose to model our species to resemble a large pelagic predator (e.g. characteristics similar to albacore (*Thunnus alalunga*, Scombridae) or swordfish (*Xiphias gladius*, Xiphiidae)) because these species have high capacity to follow changing environmental conditions, potentially leading to greater future issues with cross-boundary management, viability of home-ports, bycatch interactions, and other consequences of climate-induced range shifts (Smith, Tommasi, et al. 2021). In addition, large pelagic predators are commercially important species for US West Coast fishermen (Frawley et al., 2021) but are not routinely sampled as part of fisheries-independent surveys.

Spatial biomass of our virtual pelagic predator was simulated through a two-step process (Brodie et al., 2020). First, we simulated habitat suitability based on environmental and biological data and defined species preferences (Figure S7; see Supplementary Methods and Table S1 for more detailed information on species preferences). The environmental and biological variables used to force the species habitat suitability were SST (°C), MLD (m) and the distribution of a simulated prey species, which was forced by SST and zooplankton biomass integrated over the upper 200 m of the water column (mmol N m^{-2}). We chose to focus on the spring season, when temperatures typically warm rapidly in the northern CCS. Each variable was therefore averaged over the spring months (March–May) to capture typical spring conditions in the study system.

Step 1:
Creating virtual species
true distribution

Mixed layer depth   *Sea surface temp*   *Zooplankton 200m*

*Environmental Datasets from
NEMUCSC-ROMS*

*Generate virtual species distribution according
to a linear model of the environmental variables*

*True center
of gravity*

*True virtual
species
distribution*

Sampling (n = 100)

Step 2:
Sampling virtual
species distribution
with simulated
fishery-dependent
bias

Random Sampling   *Preferential Sampling*   *Bycatch Avoidance*

Scenario
- Bycatch
- Closed Area Lar
- Closed Area Med
- Closed Area Small
- Ports All Nearshore
- Ports All Offshore
- Ports Middle Nearshore
- Ports Middle Offshore
- Ports Northern Nearshore
- Ports Northern Offshore
- Ports Southern Nearshore
- Ports Southern Offshore
- Preferential
- Random

Closed Area   *Distance from Port*

SDMs   **GAM**
              BRT

Step 3:
Fit SDMs to simulated
data

Step 4:
Model performance
and evaluation

compare

Evaluation metrics
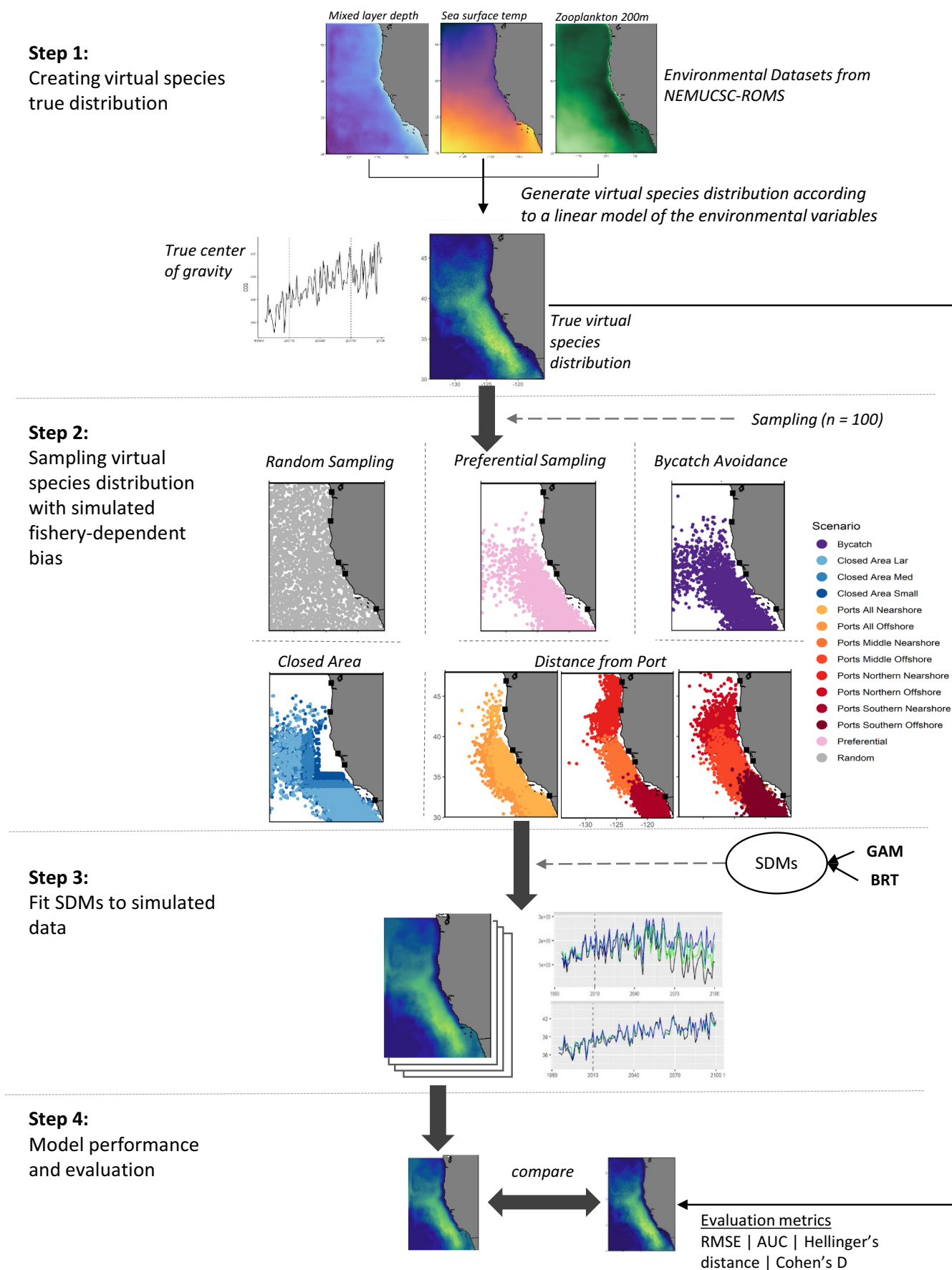RMSE | AUC | Hellinger's
distance | Cohen's D

FIGURE 2 Flow diagram illustrating the four main steps of the simulation process.

Second, habitat suitability for the simulated species was converted into presence–absence using the *probability* method in *virtualspecies*. This approach does not use a defined threshold or cut-off for presence–absence. Instead, it uses a logistic function to convert the environmental suitability of each cell into a probability of occurrence. The probability of occurrence is then used to sample presence–absence in each cell using a random draw that is weighted by the probability of occurrence (Leroy et al., 2016; Meynard et al., 2013). Biomass (kg) was then calculated as a function of the habitat suitability at locations where it was classified as present and determined to be 0 where the species was classified as absent, for each year of the simulation. Specifically, biomass was estimated from a log-normal distribution estimated from albacore (the model species for our simulated large pelagic predator) biomass in the CCS, and when the species was present, biomass at each grid cell was multiplied by habitat suitability of that same grid cell to provide habitat-informed biomass (see Table S1). Albacore biomass in the CCS was considered as the average biomass vulnerable to the US surface fleet from 1999 to 2015 (Tommasi & Teo, 2020).

2.2.3 | Sampling process: Simulating fishery-dependent data collection

We sampled the simulated species distribution according to 14 different sampling scenarios which fall under five general types of sampling types: random sampling (one scenario), preferential sampling (one scenario), constrained by distance to port (eight scenarios), constrained by bycatch avoidance (one scenario) and constrained by a closed area (three scenarios). To determine the locations of fishing activity for each of the scenarios, except *Random*, we built a 'fishing suitability' raster using a similar process as was used to build the habitat suitability rasters for our simulated species as described previously. The fishing suitability raster was used to determine the probability of each cell being sampled using the 'weights' feature within the *sampleoccurrences* function in the *virtualspecies* package. Below is an overview of the different sampling scenarios, and the full details of the generation of these fishing suitability rasters are given in Supporting Information, Material S1.

1. Random sampling: This represents our control, unbiased scenario and is closest to fishery-independent sampling. In this scenario, each cell within our study area (ROMS domain) has an equal probability of being sampled regardless of the underlying abundance of the virtual species.
2. Preferential sampling: The probability of a cell being fished is a function of the habitat suitability for the target species in the previous year (y-1), where the greater the habitat suitability the higher the probability of fishing occurring.
3. Constrained by distance to port: Suitable fishing areas are determined by distance to home ports and habitat suitability for target species. We built fishing suitability rasters for eight different distances from port scenarios: two where fishing was limited to

just around northern CCS ports (Ports Northern), two limited to around ports in the middle of the ROMS domain (Ports Middle), two limited to around southern ports (Ports Southern), and two which were not limited (e.g. fishing enabled around all ports; Ports All). One of the scenarios for each pair simulated an offshore fishery where fishing suitability was high up until about 300 miles from a port (Offshore), and one scenario simulated a nearshore fishery where fishing suitability declines after about 50 miles from a port (Nearshore).
4. Constrained by bycatch avoidance: Suitable fishing areas are determined by habitat suitability of the target species, while avoiding areas of high bycatch risk (e.g. high habitat suitability for simulated bycatch species).
5. Constrained by closed area: Suitable fishing areas are determined by habitat suitability of the target species, while taking into account that no fishing activity can occur within a static closed area. We built fishing suitability rasters for three closed area scenarios in which the size of the closed area varied (referred to as Closed Area Small, Closed Area Medium, and Closed Area Large).

These five general types represent simplified behaviour observed in actual fisheries, including some on the US West Coast. Preferential sampling represents the most ubiquitous fisher behaviour, whereby fishers follow their target species to maximize profitability (van Putten et al., 2012). Distance to port sampling is observed in the Pacific sardine fishery (Rose et al., 2015; Smith, Muhling, et al. 2021), and closed area and bycatch avoidance sampling is observed and expected in the California drift gillnet swordfish fishery (Hazen et al., 2018; Urbisci et al., 2016). We note that fishery-dependent data arises from additional processes beyond those included in the simulation model here (e.g. vertical distribution, vessel attributes, targeting and reporting rates in multispecies logbooks and area vs. effort expansion), and that there is a large literature on dealing with those additional complexities that we do not address in the SDMs fit in this study (Stephens & MacCall, 2004; Maunder & Punt, 2004; Maunder et al., 2020).

2.3 | Estimation models: Fitting species distribution models

We fit the simulated data using two types of SDMs commonly used in ecological modelling: a correlative statistical model (generalized additive model, GAM; *mgcv* R package, Wood, 2017) and a machine learning model (boosted regression tree, BRT; *gbm* R package, Elith et al., 2008). All SDMs were constructed as delta models, in which separate models are used to model the encounter probability (presence–absence) and the expected abundance conditional on encounter. All SDMs were trained on data from years 1985–2010, which we refer to as the 'historical' period, and then the fitted models were used to predict species biomass using projected environmental data for years 2011–2100. The SDMs were fit including three environmental covariates (SST, MLD, surface

chlorophyll-a) (Table S2). We use surface chlorophyll-a instead of the distribution of prey or zooplankton to avoid a perfectly specified model and mimic real-world conditions where some environmental correlates are imperfectly known. The distribution of the virtual species in the OM is directly influenced by SST, MLD, and the distribution of its prey species which is influenced by zooplankton and SST. The SDMs include SST and MLD but include surface chlorophyll-a as an indirect and imperfect proxy for prey or zooplankton. Because satellite-derived chlorophyll-a data are typically available (and prey and zooplankton data are not), this also approximates how similar models might be applied in a real-world scenario.

We evaluated the impact of alternative parameter configurations, such as including space and time covariates, on the relative influence of the different sampling scenarios on SDM performance (see Table S2 for the alternative configurations explored), but including these covariates added little to explained information (Table S2) and did not improve the spatial patterning in residuals (Figure S1) or alter the relative impact of the different sampling scenarios on model performance (Figure S2). This was likely due to the fact that the structure of our operating model could be well explained by dynamic ocean variables and did not contain much spatially structured residual information, such as known spawning grounds. Therefore, we only present and discuss the results of the BRT and GAM environmental covariate models throughout the rest of this paper.

2.4 | Assessment of climatic bias in the sampling scenarios

In order to assess the potential biases in estimates of environmental conditions created by fishery-dependent sampling, we assess both the climatic bias and climatic novelty. The climatic bias compares the sampled environmental conditions to environmental conditions throughout the entire ROMS domain during the historical sampling period (1985–2010). Climatic novelty is a measure of how similar the environmental conditions captured in each of the sampling scenarios are to the projected future environmental conditions present across the entire domain (i.e. a measure of extrapolation).

We used two metrics to obtain climatic bias and novelty, Cohen's d (cd) and Hellinger Distance (HD). Cohen's d is a measure of the distance between the means of two groups, while the HD is a measure of the difference between two probability distributions (see Cohen, 1988; Legendre & Legendre, 2012; Supplemental Methods for formulas). The HD measures how much information is contained in one distribution relative to another with values in the range [0,1]. Values of HD = 1 indicates that the two distributions have no common information (e.g. no data overlap), whereas values of HD = 0 indicates that the two distributions have the same information (e.g. complete data overlap). Johnson and Watson (2021) propose HD values >0.5 as a threshold of novelty, where the distributions become more dissimilar than they are similar. We used both of these two metrics because while Cohen's d can quantify the direction and magnitude of

the difference between means, it does not capture differences in the shape of the distributions. In contrast, though HD does not capture the direction of the difference, it can measure differences in the mean and shape of distributions. Therefore, the two metrics combine to provide an overall picture of the climatic bias and novelty.

2.5 | Model performance: Predicting abundance, centre of gravity and spatial distribution

Model estimates for species abundance and centre of gravity were compared to the simulated data, which represents the known truth, and fit and performance were evaluated using several metrics, including root mean squared error (RMSE) and Spearman correlation coefficient for continuous metrics, and the area under the receiver operating characteristic curve (AUC) for the presence/absence portions of the SDMs. AUC is a common metric to assess SDM accuracy, with values >0.75 suggesting the model provides good discrimination between locations where the species is present and where it is absent (Elith et al., 2006). SDM outputs were also compared by visually examining the predicted spatial distributions, and the model response curves for each environmental covariate (Supporting Information). For comparing performance through time, we broke the future period into three timeframes, early-century (2011–2039), mid-century (2040–2069) and late-century (2070–2100).

3 | RESULTS

3.1 | Environmental variability, sampling scenario climatic bias and novelty

The environmental variables used in the operating and estimation models exhibited both spatial and temporal variability. Surface chlorophyll, zooplankton and MLD showed a nearshore-offshore gradient, with surface chlorophyll and zooplankton concentrations being greater nearshore, while MLD was greater offshore (Figure 3). Temperature exhibited a north–south gradient, with higher temperatures in the southern portion of the domain during the historical period but increasing throughout the domain during the future period (Figure 3). In general, MLD, zooplankton and surface chlorophyll all decreased during the projection period (Figure 3). The simulated species biomass built using these environmental variables (i.e. in the operating model) also showed strong spatial patterning and was higher in southern and offshore waters. During the projection period, biomass of the simulated species increased in the northern part of the domain and decreased in the southern portion.

The geographic spatial pattern of the different sampling scenarios varied within the ROMS domain (Table 1; Figure 4), leading to differences in the environmental conditions captured in their samples. The random sampling scenario, not surprisingly, covered the largest geographic area, covering almost 90% of the ROMS domain (Table 1; Figure 4,), resulting in a wide range of environmental
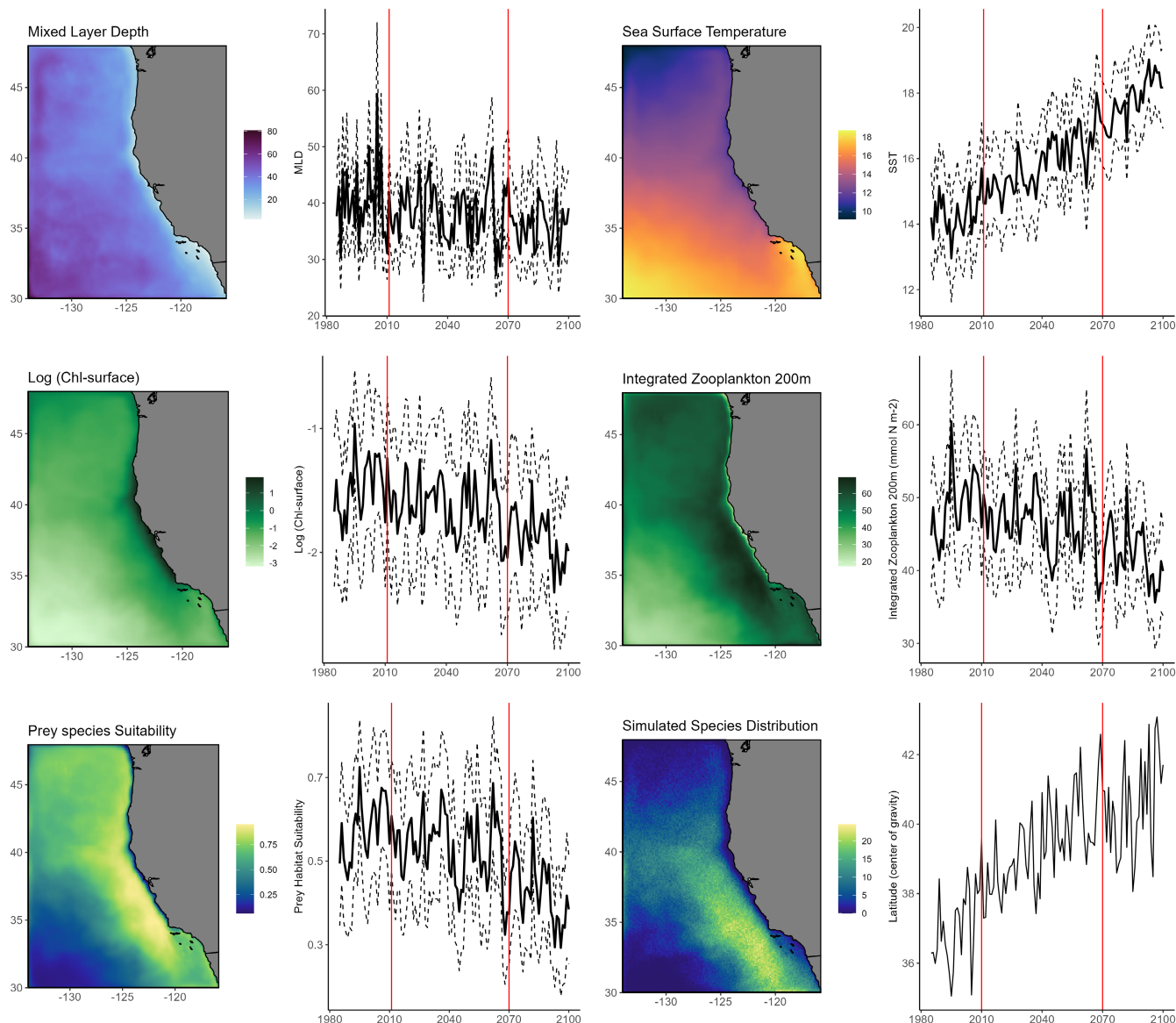
FIGURE 3 Maps and time series of dynamically downscaled environmental covariates projected to 2100. Maps show the average historical spring conditions for the dynamically downscaled environmental and biological covariates used in the operating model and/or the estimation models (mixed layer depth, SST, zooplankton, prey abundance and chl surface), and distribution of the simulated species biomass (kg) from 1985 to 2010. The time series plots show the spatially aggregated average annual spring conditions for the entire simulation time period (1985–2100). The red vertical line at 2010 indicates the beginning of the forecast period, and the red vertical line at 2070 indicates beginning of the late-century period. The dashed lines represent the mean ±1 *SD*.

conditions being sampled, and the lowest climatic biases across all environmental parameters (Table 1; Figure 5). The most biased designs were the distance from port sampling scenarios, particularly the Northern Ports Only and Southern Ports Only sampling regimes, followed by the nearshore pair of the Middle Ports and All Ports Only scenarios (Table 1; Figure 5). These sampling scenarios were the most limited in their geographical coverage, being restricted latitudinally and/or longitudinally (i.e. in the nearshore-offshore direction). Additionally, the Northern Ports Only sampling scenarios were cold-biased (cd = 0.47 and cd = 0.73) with greater sampling effort at the low temperatures and poor sampling at the high temperatures, whereas the Southern Ports Only

sampling scenarios were warm-biased (cd = −0.71 and cd = −0.97) (Table 1; Figures 5 and S2) with greater sampling at the high-temperature extremes.

In general, the environmental conditions became increasingly novel over time relative to the environmental conditions represented in each sampling scenario during the historical period (Table 2; Figure 5). For all sampling scenarios except Ports Southern Nearshore and Offshore, the climate novelty (HD and Cohen's *d*) increased through time for chlorophyll and temperature, with the largest climate novelty occurring in the late-century period (Figures 5 and S3–S5; Table 2), while climate novelty (HD and Cohen's *d*) for MLD remained low and relatively unchanged for all future time

TABLE 1 Model fit and performance (AUC, RMSE, COR), climatic bias during historical training period 1985–2010 for all environmental parameters and sampling scenarios, and the proportion of the ROMS sampling domain covered by each sampling scenario

| Sampling scenario | AUC (P) | | RMSE | | COR | | Measures of climatic bias | | | | | | Proportion area covered (%) |
| | | | | | | | SST | | Chlorophyl | | MLD | | |
	GAMs	BRTs	GAMs	BRTs	GAMs	BRTs	HD	Cohen's d	HD	Cohen's d	HD	Cohen's d	
Random	0.92	0.92	5.09	5.10	0.77	0.77	0.03	-0.07	0.05	0.06	0.03	-0.03	89.80
Preferential	0.91	0.90	5.10	5.39	0.77	0.75	0.41	-0.41	0.23	-0.20	0.17	0.05	50.18
Port Southern Offshore	0.84	0.77	6.60	8.85	0.72	0.55	0.51	-0.71	0.29	-0.32	0.26	0.39	11.55
Port Southern Nearshore	0.54	0.78	8.06	10.61	0.69	0.46	0.55	-0.97	0.32	-0.18	0.43	0.87	7.97
Port Northern Offshore	0.89	0.86	5.84	6.78	0.72	0.65	0.50	0.47	0.36	-0.45	0.25	0.23	27.25
Port Northern Nearshore	0.90	0.85	5.67	6.31	0.74	0.67	0.54	0.73	0.40	-0.50	0.35	0.55	20.28
Port Middle Offshore	0.91	0.88	5.15	5.61	0.76	0.72	0.47	-0.22	0.30	-0.42	0.21	0.08	24.70
Port Middle Nearshore	0.89	0.87	5.47	5.84	0.74	0.71	0.49	0.07	0.45	-0.85	0.25	0.21	12.11
Port All Offshore	0.91	0.90	5.12	5.37	0.77	0.75	0.40	-0.40	0.28	-0.35	0.20	0.19	30.17
Port All Nearshore	0.90	0.87	5.48	5.94	0.75	0.71	0.33	-0.17	0.37	-0.68	0.23	0.40	23.37
Closed Area Small	0.91	0.89	5.09	5.44	0.77	0.74	0.41	-0.46	0.23	-0.17	0.16	0.07	48.35
Closed Area Medium	0.91	0.90	5.07	5.26	0.77	0.75	0.42	-0.52	0.23	-0.10	0.16	0.06	40.70
Closed Area Large	0.91	0.90	5.13	5.31	0.77	0.75	0.44	-0.61	0.24	-0.07	0.16	0.12	33.88
Bycatch	0.91	0.90	5.23	5.42	0.77	0.75	0.37	-0.40	0.23	0.04	0.16	-0.12	52.53
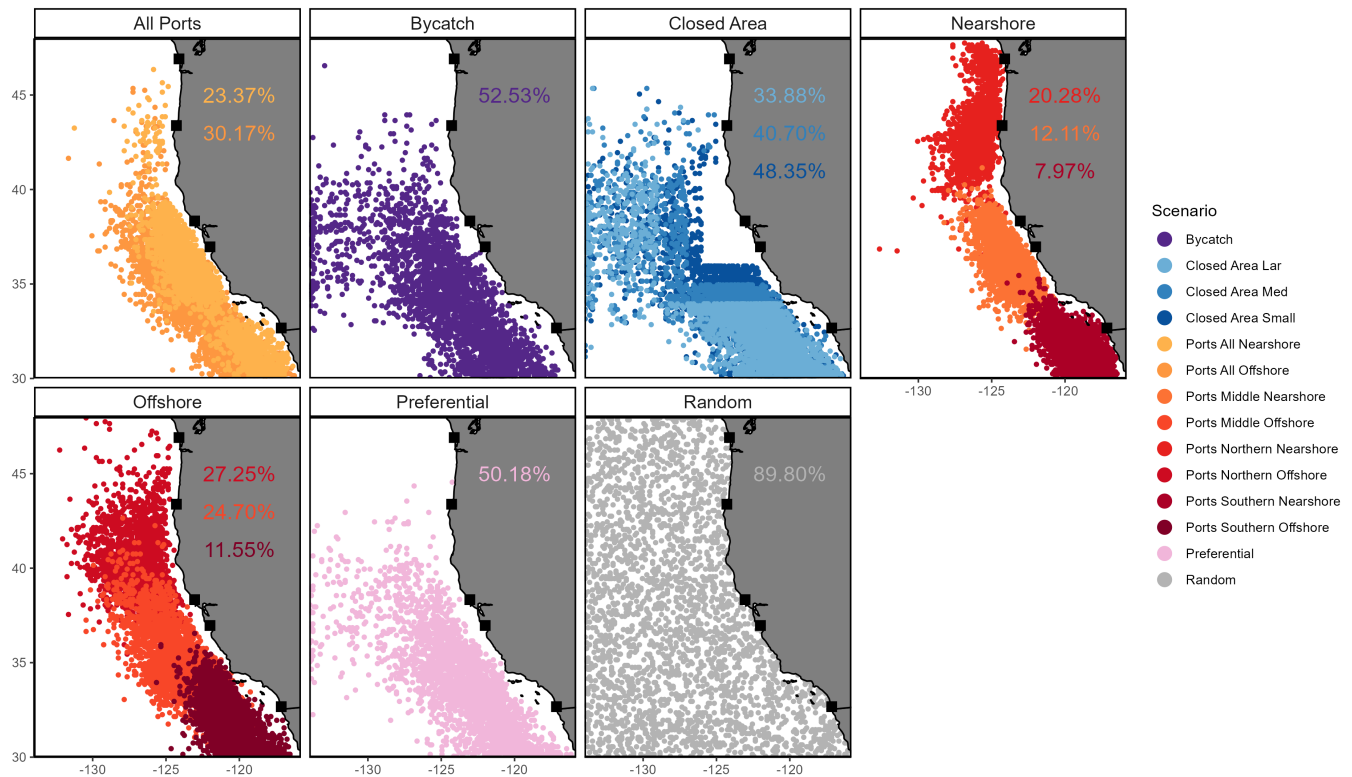
FIGURE 4 Sampling locations for each sampling scenario during the training period 1985–2010 used to fit the estimation models. The black dots indicate the locations of the ports used for the distance from ports scenarios. The percentages shown in each facet indicate the percentage of the ROMS domain covered by each sampling scenario based on the area of a concave hull around each set of sampling points.

periods (Table 2). In the early century (2011–2039), environmental conditions were novel for at least one environmental variable used in the estimation model relative to the conditions captured by three of the sampling scenarios, Ports Northern Nearshore, Ports Northern Offshore and Port Southern Nearshore. In the mid-century (2040–2069), the conditions became less novel relative to the Port Southern Nearshore sampling data, but we saw the emergence of novel conditions relative to the Middle Ports Nearshore sampling scenario for two environmental variables (temperature and chlorophyll; Table 2) and an increase in novelty relative to the Ports Northern Nearshore and Offshore scenarios. By the late-century period (2070–2100), temperature conditions were approximately novel (HD~0.5) and warmer (Figure 5, bottom panel, Table 2) than captured by all of the sampling scenarios during the historical period. Additionally, conditions were novel for two environmental parameters (temperature and chlorophyll) for four sampling scenarios, Ports Northern Nearshore and Offshore, Port Middle Nearshore and Ports All Nearshore during the late-century period (Table 2). The Ports Southern Nearshore and Offshore sampling scenarios are unique in that the HD was >0.5 for temperature during the historical sampling period (Figure 4, top panels), but then declines into the early- and mid-century, before increasing slightly again in the late-century period. While the southern sampling scenarios were warm biased relative to historical temperatures throughout the entire prediction domain, those warm-biased temperatures become more representative of the full domain in the future.

3.2 | SDM model fit and predictive skill

SDMs generally fit well to the presence–absence training data generated from the simulated fishery-independent and fishery-dependent sampling scenarios with all AUCs >0.78 for the BRTs (Araujo et al., 2005; Table 1). However, there was a noticeable difference in the predictive performance for models fit to data from the Southern Nearshore and Offshore sampling scenarios, particularly for the GAMs. Most sampling scenarios tracked the true abundance well during the historical period, except for the two Southern Ports Only scenarios which overestimated the true abundance (Figure 6). The Ports Southern Nearshore model had the lowest AUC values (0.54 and 0.78 for the GAM and BRT respectively; Table 1). One would not normally project a model which had an AUC of 0.54 as that indicates poor fit (Araujo et al., 2005; Elith et al., 2006; Swets, 1988); however, we retained the model for the purposes of this simulation.

The ability of the SDMs to replicate the known environmental affinities of the simulated species was best for models fit with the less climatically biased sampling designs (Figures S7–S14). However, only the Random and Ports Southern Nearshore sampling scenarios were able to predict the dome response curve for temperature, while other scenarios overpredicted the positive impact of high temperatures on the virtual species abundance (Figures S7 and S8). The fitted response curves generated through all other scenarios showed increasing positive partial effects on biomass at high
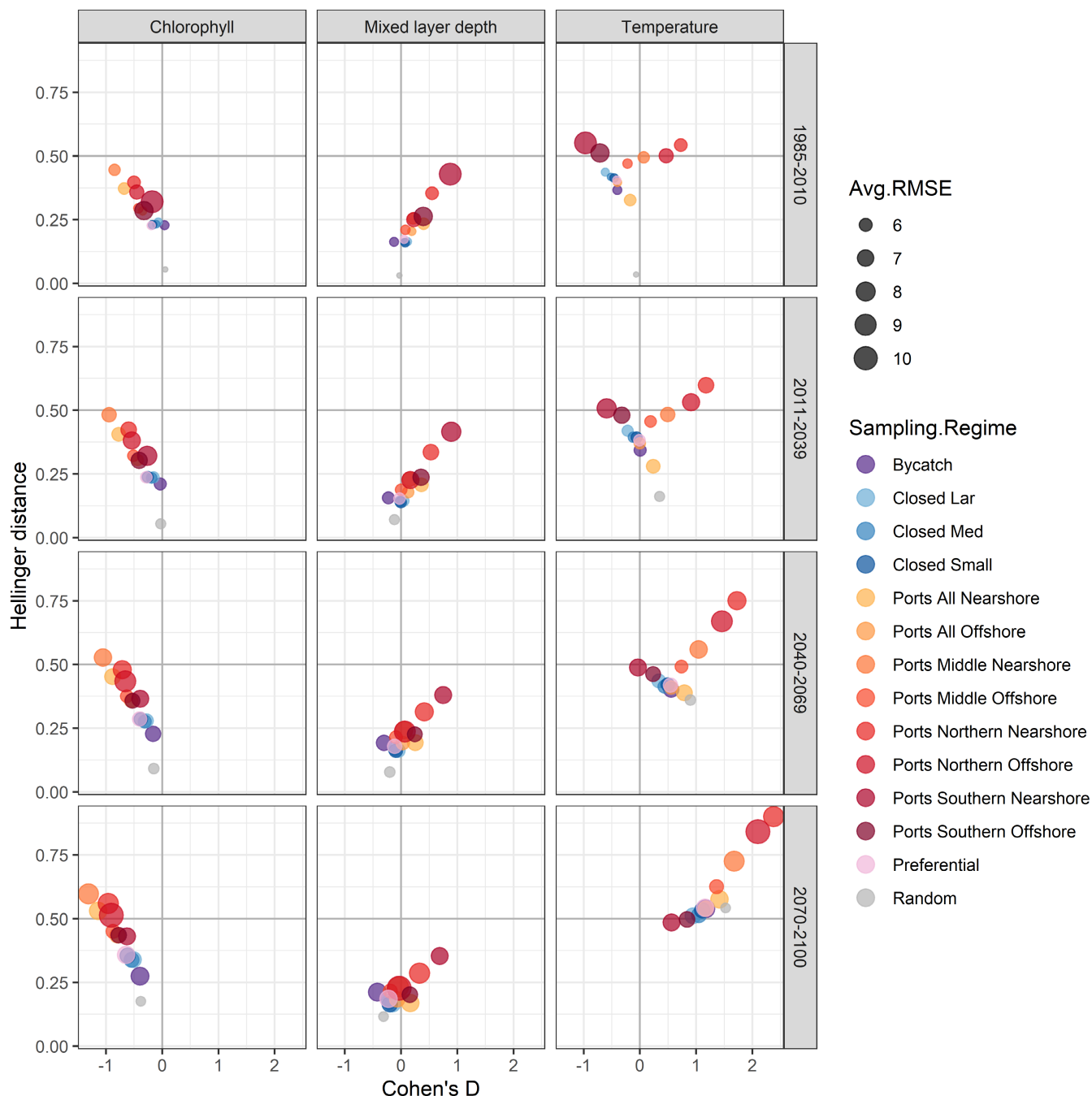
FIGURE 5 Physical climate bias (top row) and climate novelty (bottom three rows) as a function of sampling scenario. Difference in mean value (Cohen's *D*) versus difference in the sampling distribution compared to the distribution of the environmental conditions across the entire domain (Hellinger distance). Sampling data with a distribution of climate values identical to the climate values across the domain would be located at (0, 0). The size of each point is scaled by the RMSE each time period averaged over the GAM and BRT models for each sampling scenario. Negative values of Cohen's *D* (to the right of the vertical line at *x* = 0) indicate that the mean value for a parameter is greater in the sampling scenario compared to the full domain. The horizontal line at *y* = 0.5 indicates the threshold for novelty.

temperatures, instead of the decline observed in the true species response curves above 17°C. This result was most pronounced for the Ports Northern Offshore, Northern Nearshore, and Middle Nearshore sampling scenarios, which is likely due to the fact that these scenarios sampled were cold-biased (positive Cohen's *d*;

Table 1), sampling only low to mid-temperature waters and did not capture the higher temperature ranges. Models fit to data from the Ports Southern Nearshore scenario, however, were better able to capture the species temperature preferences at higher temperatures, but not at lower temperatures (Figures S6 and S7).

TABLE 2 Hellinger distance (HD) for all environmental parameters, sampling scenarios and future time periods.

Sampling scenario	Early century: 2011:2039			Mid century: 2040–2069			Late century: 2070–2100		
	Temp	MLD	Chl	Temp	MLD	Chl	Temp	MLD	Chl
Random	0.16	0.07	0.06	0.36	0.08	0.09	0.54	0.12	0.18
Preferential	0.38	0.15	0.24	0.42	0.18	0.29	0.54	0.19	0.36
Port Southern Offshore	0.48	0.24	0.30	0.46	0.23	0.36	0.50	0.20	0.43
Port Southern Nearshore	0.51	0.42	0.32	0.49	0.38	0.37	0.49	0.35	0.43
Port Northern Offshore	0.53	0.23	0.38	0.67	0.24	0.43	0.84	0.23	0.51
Port Northern Nearshore	0.60	0.34	0.42	0.75	0.31	0.48	0.90	0.29	0.56
Port Middle Offshore	0.46	0.19	0.32	0.49	0.21	0.37	0.63	0.22	0.45
Port Middle Nearshore	0.48	0.23	0.48	0.56	0.24	0.53	0.73	0.23	0.60
Port All Offshore	0.37	0.18	0.30	0.41	0.19	0.36	0.54	0.18	0.44
Port All Nearshore	0.28	0.21	0.41	0.39	0.19	0.45	0.58	0.17	0.53
Closed Area Small	0.39	0.14	0.24	0.42	0.16	0.29	0.53	0.16	0.36
Closed Area Medium	0.39	0.14	0.23	0.41	0.17	0.28	0.51	0.17	0.34
Closed Area Large	0.42	0.14	0.24	0.44	0.16	0.28	0.51	0.16	0.34
Bycatch	0.34	0.16	0.21	0.40	0.19	0.23	0.54	0.21	0.27

Note: The HD for the future periods provides an indication of the novelty of the environments during those future periods relative to the environment conditions captured by each sampling scenario during the historical period. The colours represent the degree of climate novelty, with novelty increasing as the colors move from green (lowest), to yellow, to red (highest).

3.3 | SDM projection performance

In our study, model performance (RMSE) tended to decline with increasing HD (Figure S15), and in general, SDM performance (as determined by RMSE, correlation, model uncertainty, and spatial error) was the worst during the period when climatic bias and novelty was greatest. For most scenarios, this occurred during the late-century period, but for the two Southern Ports Only scenarios it was during the historical training period.

Many of the models fit to data collected from a fishery-dependent sampling scenario (Preferential, Bycatch, Closed Area Small, Closed Area Medium, Closed Area Large, Ports All Offshore, Ports Middle Offshore) performed comparably to the Random sampling scenario, tracking the true biomass well during the early- and mid-century projection periods (Table 3; Figure 6a,b). However, these sampling scenarios exhibited a more pronounced decline in performance (increasing RMSE (Table 3; Figure S16), decreasing correlation (Figure S17), and increasing uncertainty (Figure S18)) during the late-century period compared with the random sampling scenario (Table 3). Models built with more climatically biased training data performed less well. The worst performing models were those fit to data collected from the Ports Northern Nearshore, Ports Northern Offshore, Ports Middle Nearshore, Ports Southern Nearshore and Ports Southern Offshore sampling scenarios (Table 3; Figure 6a,b). An interesting observation, however, is that while performance declined throughout the projection period for Ports Northern Nearshore, Ports Northern Offshore and Ports Middle Nearshore, it improved somewhat for the Ports Southern Offshore and Ports Southern Nearshore scenarios,

probably because environmental conditions were actually becoming less novel (compared to those sampled) for the southern sampling scenarios.

Models that were best able to track biomass during the early and mid-century periods were also best able to track the true centre of gravity during the early-century and beginning of the middle-century periods (Preferential, Bycatch, Closed Area Small, Closed Area Medium, Closed Area Large, Ports All Offshore, Ports Middle Offshore; Figure 7a,b). These models predicted centre of gravities within 1 degree latitude on average of the true centre of gravity through the early and mid-century, before diverging from the true centre of gravity trend and beginning to underestimate the northward shift by more than 1 degree during the late-century periods (Figure 7b). The most highly climatically biased scenarios (Ports Middle Nearshore, Port Northern Nearshore and Port Northern Offshore) on the other hand began underestimating the true centre of gravity by more than 1 degree starting in the mid-century and by the late century they underestimated the true centre of gravity by as much as 2.4–3.2 degrees. The Southern Nearshore and Offshore scenarios were unique in that they overestimated the centre of gravity by almost 2.6–2.7 degrees during the historic period and then underestimated the centre of gravity throughout the future periods (Figure 6b).

Spatially explicit predictions of biomass were also comparatively similar across sampling procedures and resembled the true abundance distribution during the historical and early and mid-century future periods (Figures 8 and S19–S22). In the late-century period, all sampling scenarios overpredicted the true biomass in the southern, warmer part of the CCS. The exception to this was models fit to
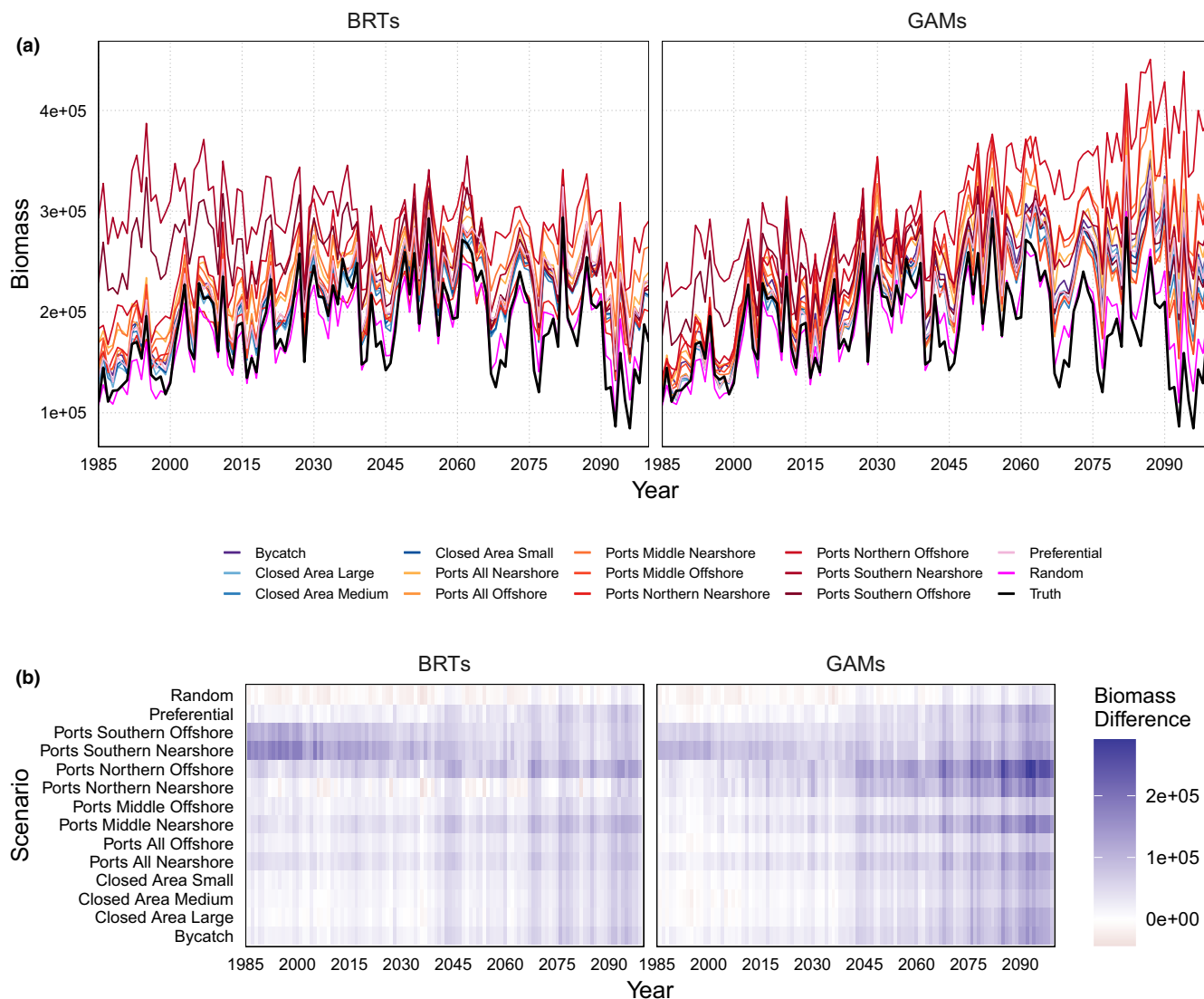
FIGURE 6 Biomass time series for 1985–2100 showing the true biomass, each of the 14 scenarios for the GAMs and BRTs (a) and the difference between the true biomass and biomass predicted with each of the scenarios across the time series (b).

data collected under the Ports Northern Nearshore, Ports Northern Offshore, Ports Middle Nearshore and Ports All Nearshore sampling scenarios, which overpredict the biomass of the species in the southern part of the ROMS domain throughout the entire time series, with the greatest overpredictions in the late-century period. Additionally, models fit with data collected under the Ports Southern Nearshore and Offshore sampling scenarios overpredict the biomass in the northern part of the domain throughout the time period (Figures 8 and S19–S22), as well as overpredicting the biomass in the southern part in the middle and late century. Again, this likely occurred because models fit with Southern Ports Only data do not accurately represent the species temperature response curve at lower temperatures; similarly, models fit using the other sampling scenarios do not accurately represent the species temperature response curve at intermediate and higher temperatures, and this is particularly true for the two Northern Only and the Middle Nearshore Ports scenarios.

4 | DISCUSSION

As climate change leads to increasingly novel ocean conditions (Gruber et al., 2021; Smith et al., 2022), it is important to understand how fish and other marine organisms will respond to those changes. Realistic projections of potential future species distributions are important to categorize species responses and to be able to prepare for and sustainably manage for distribution shifts. However, there is limited understanding of how well models perform when projecting decades into the future, particularly when training data come from varied sources, such as with fishery-dependent data. In this study, we showed that use of non-randomly sampled data can have relatively minor impact on SDM performance for near- to medium-term projections as long as it samples well the underlying environmental conditions present. We further established that, regardless of sampling design, SDM performance tends to degrade for long-term projections (RMSE = 5.5–8.6 vs. RMSE = 5.3–12.6, during early and

TABLE 3 Root mean squared error (RMSE) of modeled and 'true' biomass, by time period and sampling scenario.

Sampling scenario	2011–2039		2040–2069		2070–2100	
	GAM	BRT	GAM	BRT	GAM	BRT
Random	5.47	5.50	5.55	5.52	5.50	5.30
Preferential	5.61	5.79	6.56	6.25	8.15	6.56
Port Southern Offshore	6.47	7.50	6.60	6.39	7.35	6.09
Port Southern Nearshore	7.46	8.85	7.26	7.07	8.05	6.37
Port Northern Offshore	7.29	7.31	9.73	7.89	12.59	8.24
Port Northern Nearshore	6.67	6.84	8.24	7.12	9.98	7.02
Port Middle Offshore	5.61	5.78	5.97	5.97	6.49	6.08
Port Middle Nearshore	6.47	6.27	7.97	6.72	9.69	7.11
Port All Offshore	5.67	5.69	6.28	5.98	6.99	6.28
Port All Nearshore	6.26	6.17	7.28	6.30	8.41	6.39
Closed Area Small	5.62	5.68	6.40	5.88	7.39	5.98
Closed Area Medium	5.55	5.57	6.23	5.79	7.16	5.92
Closed Area Large	5.61	5.63	6.45	5.94	7.64	6.03
Bycatch	5.84	5.81	6.99	6.25	8.60	6.57

Note: The colours indicate the relative size of the error among sampling scenarios, with greener colours reflecting lower errors, redder colours reflect higher errors, and yellows in between.

late century respectively), due to the higher climatic novelty of the future environmental conditions relative to the sampling data.

4.1 | Differences among sampling scenarios

A major concern with fishery-dependent data used to estimate species distributions is the potential biases due to the unequal sampling, as fishers tend to preferentially target locations with high density of specific fishes and respond to external economic and management factors rather than randomly sampling. However, our results show that data generated from fishery-dependent sampling can still result in SDMs with performance comparable to SDMs generated from random samples several decades into the future, given specific forms of preferential sampling which result in low climate bias and novelty (e.g. HD <0.5). Preferential, Closed Areas, Bycatch and Ports Middle Offshore, Ports All Offshore all had low climate bias in the training data, and models fit to these data performed similarly to each other, and to the Random sampling scenario before degrading around mid to late century (e.g., RMSE 5.55–6.99 vs 5.47–5.5 respectively). On the other hand, the Southern Ports Only and Northern Ports Only scenarios had the highest climate bias or novelty and performed poorly throughout the projection period. By evaluating our range of scenarios, generalizations can be made about the causes of poor SDM performance and magnitude resulting from biased sampling. These generalizations relate to how well fishery-dependent data leads to correctly specified species-climate response curves, and how well these data represent the environmental conditions that exist in the data set used for prediction.

Our findings were consistent with numerous studies which show that restricting the range, and particularly the extremes, of environmental data present in a sample can affect the calculation of species-climate response curves and can lead to erroneous projections (Hortal et al., 2008; Nazzaro et al., 2021; Støa et al., 2018; Tessarolo et al., 2014; Thuiller et al., 2004). This is likely to occur in systems with strong geographic or temporal gradients in environmental variables when only a portion of the domain or a portion of the habitat or only certain seasons or years are sampled. For example, this was particularly evident for the Northern Ports Only and Southern Ports Only scenarios, where the environmental range covered in the samples was restricted to either cold (northern ports) or warm (southern ports) waters. This led to inaccurate prediction of the species responses to warm temperatures for the northern ports scenario, and to cold temperatures for the southern port scenario. If a response to a particular environmental covariate is non-linear (e.g. our domed preference for SST, Table S1), high sampling coverage across a range of covariate values may be required to fit that response correctly. Often there will be reduced data coverage and increased model uncertainty at the limits of this response. This uncertainty will be exacerbated if extrapolation of this response is required during prediction or projection, which can be seen in our study in Figure S18. Therefore, one should be careful or critical when an estimated relationship to an environmental variable is approximately linear across the training data, particularly if it is a positive linear relationship.

Training data quality is also acknowledged to be a key issue determining the transferability of SDMs to novel locations or environments (Elith & Leathwick, 2009; Sequeira et al., 2018; Yates et al., 2018). We measure this as both climatic bias (how well the historical climate was sampled in our domain of interest) and climatic novelty (how well the sampled historical climate represents future conditions used for projection). We also estimated the spatial area covered by each sampling scenario (Figure 4), and this tended to be a good indicator of the subsequent climatic bias, with scenarios that
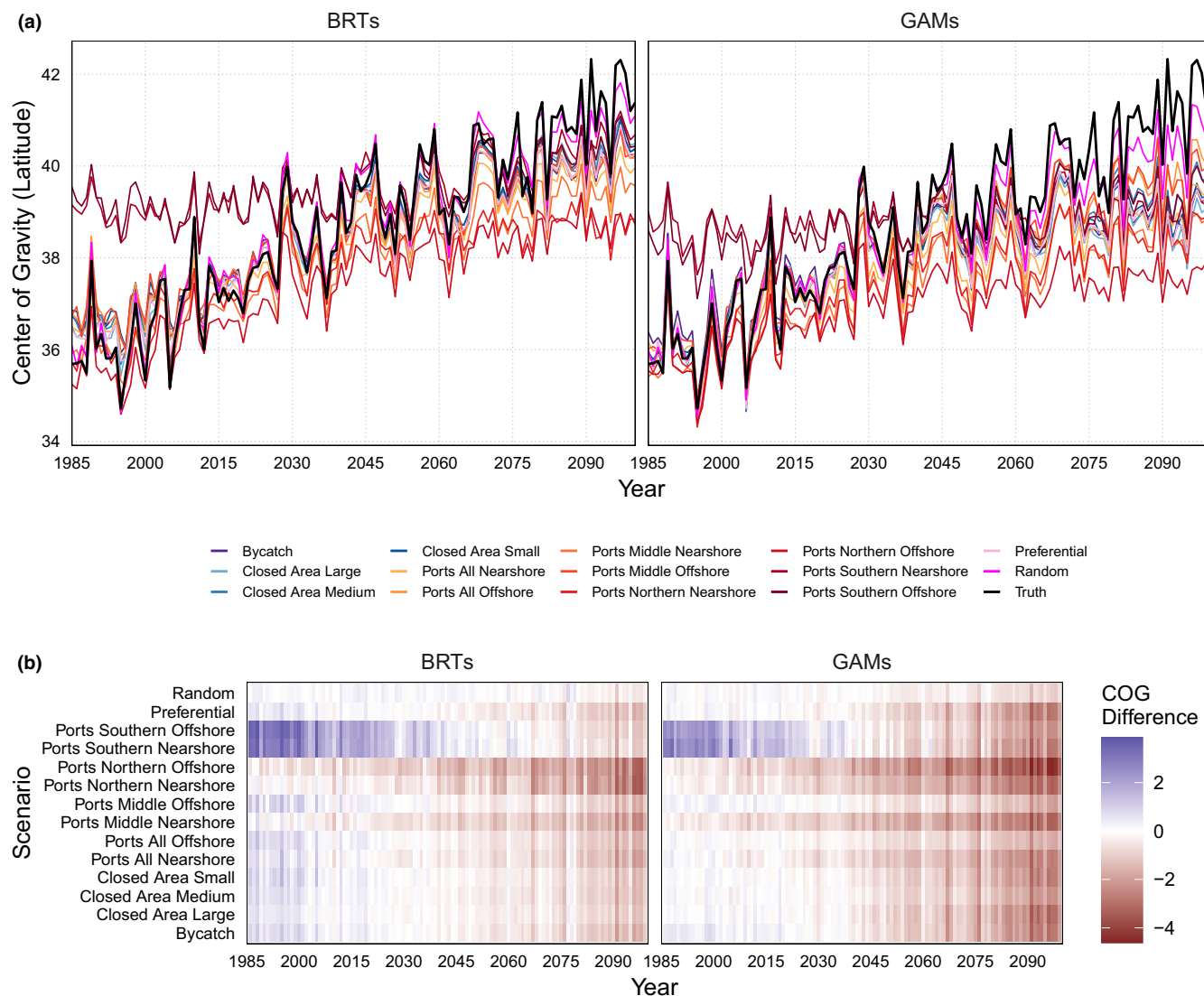
FIGURE 7 Latitudinal centre of gravity time series for 1985–2100 showing the latitudinal centre of gravity, each of the 14 scenarios for the GAMs and BRTs (a) and the difference between the true centre of gravity and centre of gravity predicted with each of the scenarios across the time series (b).

sampled a higher proportion of the ROMS domain, tending to have lower climatic bias of the sample; however, this was not always the case (Table 1). This is consistent with previous studies which conclude that the underlying environmental conditions sampled is more important than the spatial structure of samples in terms of effecting SDM performance (Tessarolo et al., 2014) and supports the use of a climatic bias measure, such as the HD, as a metric of data quality and potential indicator of SDM performance rather than the spatial coverage of a sample set.

Higher climatic bias in the sample data led to either poorly fit models (e.g., Southern Port Nearshore, AUC = 0.53, RMSE average = 9.34) and/or poor performance, and more quickly degrading performance, when projecting into future, novel conditions. Models fit to data from sampling scenarios with high climatic bias during the training period (Northern and Southern Ports only, Middle Nearshore and All Nearshore) resulted in RMSEs during

the early and mid-century period that were 14–75% greater relative to random sampling, whereas the less climatically biased scenarios resulted in RMSE that were only 1–18% greater compared with the random sampling scenario. By the late century period, all SDMs except for those fit to the Random sampling scenario showed declining performance; however, this decline in performance was greater for the more climatically biased sampling with RMSE increasing to 33–128% greater than the random sample compared with only 11–56% greater for less biased scenarios. This suggests that SDMs will likely show degrading performance over time given high climatic novelty in future periods, although random sampling can help mitigate this (Figure 6; Table 3). We note that the amount of extrapolation into the future, and thus the impact on model predictive skill, varies among climate models (see Brodie et al., 2022) and scenarios. In our simulation, we used the HadGEM2-ES ESM, which exhibits some of the fastest warming
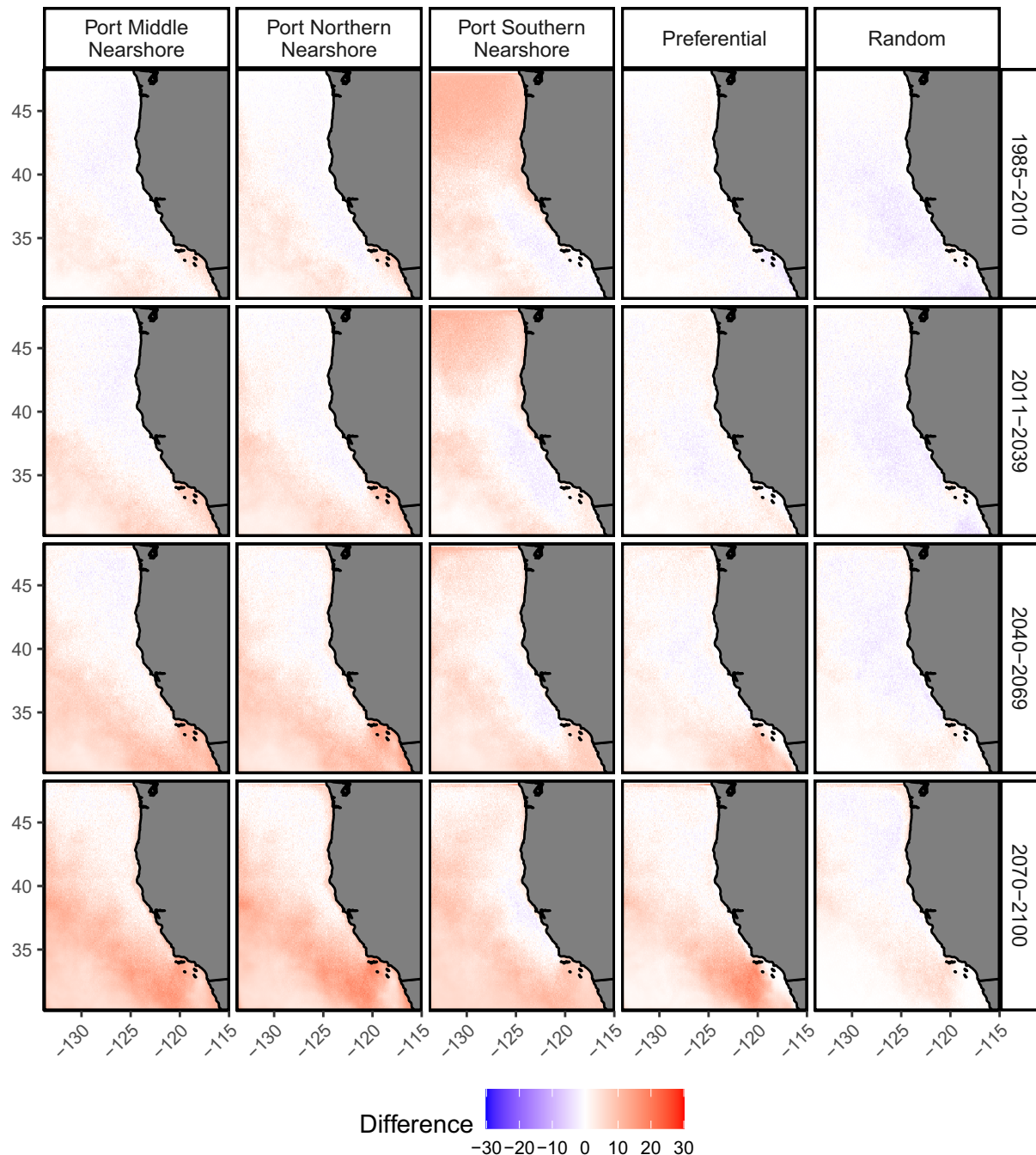
FIGURE 8 Maps of difference in the predicted species distribution averaged across the historical period (1985–2010; top panel) and each of the future periods (2011–2039, 2040–2069 and 2070–2100). Here, we show the spatial differences between the predicted distributions from two sampling scenarios with low climate bias, the random and preferential sampling, and three sampling scenarios with high climate bias, ports southern nearshore, ports middle nearshore and ports northern nearshore, fit with a GAM, compared with the true simulated distribution. See Figures S19–S22 to see spatial differences for all sampling scenarios. Red areas indicate areas where the model overpredicts the biomass, and blue areas where the model underpredicts the biomass.

and productivity declines for the CCS (Pozo Buil et al., 2021) and thus higher novelty (Smith et al., 2022). Thus, while in our study SDM projection performance began to degrade mid-century for many scenarios, other studies may see performance degrade earlier or later depending on which ESM is used (Brodie et al., 2022). Our results suggest that this degradation in performance may occur when the conditions for at least one climatic variable used in the model become more dissimilar than similar (i.e. HD ~ 0.5) to the conditions represented in the training data.

Our results are based on a simplified simulation framework designed to test the predictive performance of SDMs fit to simulated fishery-dependent data, and as such there are several important assumptions and caveats to note. First, the scenarios simulated in our study are a simplified version of fishery-dependent data collection.

There are several factors that we have not captured in our simulation which can impact both where and how much fishermen catch (e.g. density dependence, interspecific interactions, catchability, fisher behaviour and market dynamics), and therefore the relative bias and performance of models fit to that data. Future studies could work to incorporate these dynamics into simulations. Additionally, we simulated a mobile pelagic species, which has the advantage of not having to consider benthic habitat requirements (the animal can just move to follow favourable conditions). Simulating benthic or demersal species realistically might be more difficult. Additionally, how a species is distributed in space and time can be determined by more than just environmental conditions. Other important drivers could include, life history and the complexity of the life cycle, the presence of specific habitat requirements, trophic interactions and competition. For example, a diadromous species exhibiting natal homing may have clear thermal and other environmental preferences but have less ability to shift its distribution than a species which completes its entire lifecycle in the epipelagic zone. Exploring the impact of these additional drivers of species distributions on SDM performance given different sampling scenarios is beyond the scope of this study, but may be a fruitful endeavour for future simulations. Lastly, while our simulation focuses on the CCS, the general conclusions with regard to the relationship between the climatic bias of the training data and climatic novelty of the future conditions and performance of SDMs can be of use to other systems. However, we would expect that the specific sampling patterns that may lead to climatically biased data will depend on the spatial gradient of the environmental conditions and factors influencing species distributions and fishing patterns within a specific system.

4.2 | Applications and recommendations

Although fishery-dependent data are inherently biased, they can still be useful for SDMs and projection, especially if we can account for this bias through careful model specification or by restricting predictions to the geographical or environmental space covered by the model training data (e.g. Crear et al., 2021). For example, warming is one of the key climate drivers in long-term projections. If our fishery-dependent observations cover a broad range of a species' thermal tolerance, and if the behaviour of the SDM near the upper thermal limit corresponds well with known physiological limits, then projections of habitat change due to warming are likely to be more accurate. This also applies to other important environmental drivers, such as dissolved oxygen and pH, and is in line with Elith et al. (2011) and Støa et al. (2018) which posit that good SDM performance relies on the distribution of the sampling effort being proportional to the actual frequency distribution of environmental conditions along all environmental variables of importance to the species, which can be indicated through the use of the HD and cd as done in this study. On the other hand, an SDM is less likely to provide realistic projections if the observations sample a relatively small portion of the species geographic or environmental range, if detectability on fishing gear is imperfect or inconsistent, or if SDM covariates do not represent key processes well (such as obligate prey following or other trophic interactions that are not directly linked to environmental variables).

We have shown that climatic bias and novelty are useful measures of impact of available observations on the performance of SDM projections. These or similar metrics (Mesgaran et al., 2014; Meyer & Pebesma, 2021; Smith et al., 2022) are critical components of projection studies because they allow estimation of how no-analogue environmental conditions relate to predictive skill. However, consideration of how different modelling methods behave when extrapolated is also essential, as some are better suited to extrapolation. The two methods used in this study (BRTs and GAMs) predict to novel conditions differently. GAMs (depending on how they are parameterized) can continue fitted trends into new environments, whereas BRTs assume a constant relationship outside of the training data range (Zurell et al., 2012). Our results show that GAM and BRT projections often diverged strongly towards the end of the 21st century for more biased sampling scenarios, as environmental conditions became more novel. Although this is particular to our study, projections from BRTs were generally closer to the simulated truth, probably because of their more conservative behaviour under extrapolation. Other studies (e.g. Derville et al., 2018; Moore et al., 2016; Zurell et al., 2012) indicate that BRTs do not always outperform GAMs, and that the best SDM for a particular purpose tends to be highly species- and ecosystem-specific. Overall, the use of an ensemble of different SDMs is likely useful for capturing some of the uncertainty contributed by model extrapolation behaviour when predicting in novel environments. Predictions from different types or parameterizations of SDMs can be ensembled and weighted based on some measure of model fit or uncertainty (e.g. Yao et al., 2018).

Accounting for bias in fishery-dependent data through model specification has a rich history, driven by models aimed at catch-per-unit-effort standardization and calculating abundance indices (Maunder & Punt, 2004; Thorson et al., 2020). Spatial and temporal biases in these data (such as a spatial shift in fishing effort) are often accounted for by including spatial and temporal covariates (Ducharme-Barth et al., 2022), which are used to explain unknown biological processes or to act as latent variables to explain residual dependencies. These studies focus on standardizing observed data to explain historic patterns of spatial distributions and abundance. However, these spatial–temporal standardization tools may be unsuitable for long term projection of species distributions, given that static spatial surfaces and covariates incorporating year effects used to explain the past may not extrapolate well to future conditions. Indeed, some covariates can act as surrogates for variables or processes that may diverge over time and result in poor projections of species distributions. And yet, the benefits of spatial–temporal modelling not only include the potential to reduce bias in fishery-dependent observations but also the 'borrowing' of nearby information to improve the accuracy of spatial–temporal extrapolation (Brodie et al., 2020; Thorson, 2019 [VAST]). We note that when we evaluated the impact of including space and time covariates on the

relative influence of the different sampling scenarios on SDM performance, including these covariates added little to explained information (Table S3), and did not improve the spatial residual pattern (Figure S1) or alter the relative impact of the different sampling scenarios on model performance (Figure S2). However, there is potential for other parameterizations of the space and time covariates to have different results and considering the potential benefits and successes in reducing bias seen in other studies, further exploring the use of spatio-temporal modelling for SDMs using fishery-dependent data is still warranted. Another approach that has shown promise to reduce bias from preferential sampling data is to use a modelling framework where the state variable of interest (e.g. population biomass or abundance) and the sites chosen for sampling are jointly modelled using a dependence covariance matrix (Conn et al., 2017). Future work could also consider this analytical approach to explicitly account for biases from fishery-dependent sampling.

The challenge remains, then, to decide how much extrapolation in time (years or seasons) or space is acceptable, and these variables can be included in measures of novelty (Smith et al., 2022) to aid this decision. However, in terms of projecting into novel conditions, geographic and temporal separation between the reference and target system appears less important compared with environmental dissimilarity (Yates et al., 2018). In this paper we show how Hellinger Distance can be used as a measure of this environmental dissimilarity, with values around the 0.5 threshold proposed by Johnson and Watson (2021) serving as an indication of when projections (transferability) may become problematic. Again, we note that the amount of extrapolation into the future that might be appropriate may vary among climate models and exploring the dissimilarity (or similarity) in future climate projections could be informative to future management scenario planning.

When projecting SDMs built from fishery-dependent data, we recommend to (1) collect training data from the broadest range of environmental conditions relevant for a species (Pennino et al., 2016), which may require combining fishery-independent and dependent data sets (e.g. Alglave et al., 2022; Rufener et al., 2021); (2) use one or more diagnostics to identify biased data, severe extrapolation, and potentially inaccurate predictions (e.g. our Hellinger D threshold); (3) evaluate the plausibility of the partial species-climate responses, especially at the limits of the fitted data and when extrapolated to novel data; (4) explore spatio-temporal modelling, and other analytical approaches, to reduce bias in training data, but evaluate the benefits against the reduced flexibility of spatial–temporal variables for long-term projection; (5) measure and communicate uncertainty of projections, but recognize that if data are biased and a model is poorly specified then uncertainty may be underestimated.

5 | CONCLUSION

We show that SDMs built using data collected from a simulated fishery can produce projections of species distributions similar to SDMs fit with data collected from a random sampling scheme, as long as the sampling adequately captures the underlying environmental conditions present in the prediction domain. Being able to diagnose and understand when fishery-dependent data is of high enough quality (e.g. low climate bias and novelty, in addition to accurate location and catch reporting) to produce accurate predictions can help open the door for scientists and managers to use more of the observational data available to them and to more fully understand the uncertainty associated with using this data for predictions and projections of species distributions.

The use of fishery-dependent data, either on its own or in conjunction with fishery-independent data, has several benefits. For example, fishery dependent data are often collected at higher spatial and temporal resolutions than fishery-independent survey data. Unbiased fishery-dependent data (e.g. with low climate bias and novelty), or fishery-dependent data bias corrected through the use of spatio-temporal modelling as discussed above or other bias correction approaches, may thus be our best way of linking fish distributions to seasonal and spatial processes such as physical drivers of recruitment (e.g. preconditioning of mature females; Haltuch et al., 2020; Tolimieri et al., 2018) or seasonal/long-term changes in habitat characteristics like temperature, dissolved oxygen, stratification, seascape characteristics (Pennino et al., 2016). Additionally, having distribution data from many seasons will help to parameterize seasonal species distribution expectations in end-to-end models that support ecosystem-scale management strategy evaluations, for example focused on robustness of management structure to species distribution shifts driven by climate events and climate change (Kaplan et al., 2021). Synthesizing outcomes across fishery-dependent and independent data can help support the Ecosystem-Approach to Fisheries Management (EAFM) or Ecosystem-Based Fisheries Management (EBFM), through incorporating fishers' knowledge (e.g. local ecological knowledge) along with any additional data they may be able to collect in the future as ships of opportunity for monitoring environmental conditions. Finally, as costs and financial resources for fishery-independent surveys are increasingly limited in many areas, fishery-dependent data may be able to supplement information from surveys that are reduced or eliminated for budgetary reasons (though not without potential cost to the usefulness of the data).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.