Groundfish biodiversity change in northeastern Pacific waters under projected warming and deoxygenation

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Abstract

Projections of how climate change will impact marine species and communities are urgently needed to inform management measures aimed at stemming biodiversity loss. In the coming decades, warming and deoxygenation of marine waters are anticipated to result in shifts in the distribution and abundance of fishes, with consequences for the diversity and composition of fish communities. Most projections to date have focused on temperature, but have not accounted for the confounding influence of oxygen and depth and are limited by the spatial resolution of global climate models. Here, we combine fisheries independent trawl survey data spanning the west coast of the USA and Canada with high resolution regional ocean models to make projections of how 40 groundfish species will be impacted by changes in temperature and oxygen in British Columbia (B.C.) and Washington. By leveraging coast-wide survey data, we quantify how temperature, oxygen, and depth jointly constrain the ranges of species. Then, using two high-resolution regional ocean-biogeochemical models, we make projections of biodiversity change at a high spatial resolution. Our projections suggest that, in B.C. and Washington, the number of species that are projected to decrease in occurrence is roughly balanced by the number that are projected to increase, resulting in considerable compositional turnover. Many, but not all, species are projected to shift to deeper depths as conditions warm, but low oxygen will limit how deep they can go. Thus biodiversity will likely decrease in the shallowest waters (< 100 m) where warming will be greatest, increase at mid depths (100—600 m) as shallow species shift deeper, and remain stable or decrease at depths where oxygen is limited (> 600 m). These results highlight the critical importance of accounting for the joint role of temperature, oxygen, and depth when projecting the impacts of climate change on marine biodiversity.

Keywords: climate change, regional ocean model, species richness, temperature, dissolved oxygen, hypoxia, depth, species distribution

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Introduction

In marine ecosystems, climate change is expected to result in warmer waters and reduced dissolved oxygen, both of which are likely to impact organismal performance, population growth rates, and viability (Prince *et al.* 2010; Deutsch *et al.* 2015). There is evidence that marine species are more sensitive to temperature changes than terrestrial species and many species are already shifting their distributions to track changing conditions (Poloczanska *et al.* 2013; Pecl *et al.* 2017; Pinsky *et al.* 2021). Therefore, we expect to see considerable reorganization in the composition of marine communities as conditions continue to change (Bartley *et al.* 2019; Pinsky *et al.* 2020). Projections of how species and communities will respond to climate change over the coming decades are needed in order to develop management strategies for preserving biodiversity and ensuring the sustainability of fisheries and ecosystems (Wilson *et al.* 2020).

Species distribution models (SDMs), which leverage current species–environment associations across space to make projections of how species will respond to temporal changes in climate, are increasingly being applied in marine environments. These models generally project that species' ranges will shift polewards as conditions warm (García Molinos *et al.* 2016). Range shifts for species in west coast North American waters are projected to be particularly large, with many species' range limits expected to change by more than 1000 km by the end of the century under high greenhouse gas emissions scenarios (Morley *et al.* 2018). This result is consistent with estimates that suggest that the range edges of marine species are generally, but not universally, changing with warming ocean water temperatures (Sunday *et al.* 2012; Fredston *et al.* 2021). In Canadian Pacific waters, there is evidence that changes in temperature and oxygen are impacting the distribution and densities of groundfish species (English *et al.* 2021), but that these changes have not yet resulted in major changes in the diversity and composition of the groundfish community (Thompson *et al.* 2022).

The robustness of SDMs depends on properly accounting for, and distinguishing, the influence of multiple environmental variables on species distributions. In marine environments we know that species are strongly influenced by temperature and dissolved oxygen (Prince *et al.* 2010; Brown & Thatje 2015; Deutsch *et al.* 2015), both of which are projected to change in the coming decades (e.g., Holdsworth *et al.* 2021). However, most SDM models to date do not account for oxygen (e.g., Cheung *et al.* 2009; Ready *et al.* 2010; Morley *et al.* 2018), and in some cases, rely on sea surface temperature, when modeling species that live on the seafloor (e.g., Ready *et al.* 2010; García Molinos *et al.* 2016). In addition, demersal marine communities (e.g., groundfish) are highly depth structured because of physiological limits to temperature, hydrostatic pressure (Brown & Thatje 2014), and hypoxia tolerance (Brown & Thatje 2015), as well as light, competition, and food availability (Elith & Leathwick 2009). However, because depth, temperature, and oxygen are closely correlated in many regions, it can be challenging to distinguish the role of each of these variables in determining contemporary species distributions. Some models have addressed this challenge by assuming that depth distributions are entirely determined by temperature because this allows for projected distributions to shift into deeper waters as conditions warm (Pinsky *et al.* 2013; Morley *et al.* 2018). However, if depth—and associated variables (e.g., light and pressure)—influences species ranges directly as well as by influencing water temperature and dissolved oxygen, then the direct effect of temperature and dissolved oxygen on species ranges cannot be determined without also accounting for the independent influence of depth.

Although climate SDM studies often focus on range shift rates and distances, climate change will also impact species within their range boundaries (English *et al.* 2021). Projections that capture local scale changes in species' occurrences and abundances are particularly needed for the implementation of climate resilient management strategies such as establishing networks of marine protected areas and fisheries management areas (Wilson *et al.* 2020; O'Regan *et al.* 2021). The recent development of regional ocean models that downscale climate projections at a high-resolution (e.g., Peña *et al.* 2019; Holdsworth *et al.* 2021) offers the opportunity to make projections at spatial resolutions (e.g., <3 km) that are relevant to marine spatial planning initiatives (Frazão Santos *et al.* 2018; Gissi *et al.* 2019; Friesen *et al.* 2021).

Here we provide projections of groundfish community change in British Columbia (B.C.), Canada and Washington, U.S.A. waters under future climate change scenarios (2046–2065) that account for the combined effects of temperature, dissolved oxygen, and seafloor depth at a spatial scale that is relevant to marine spa-

tial planning and fisheries management. We do this by using SDMs to estimate how temperature, oxygen, and seafloor depth determine the current occurrence and distribution of 40 groundfish species across the west coast of North America from California to Alaska (Figure 1a), based on fisheries independent trawl surveys. We then combine these estimated species responses with two regional ocean models that cover B.C. and Washington waters to project changes in species occurrences from a historical baseline of 1986–2005 to a future period in 2046–2065 under Representative Concentration Pathways (RCP) 4.5 and 8.5 (Figure 1). Estimating species' responses to the environmental variables using the spatially extensive trawl survey dataset allows us to capture the majority of species' ranges, and to explore a wider range of environmental conditions than are present in the region where we make our projections. In particular, the tight correlation between depth, temperature, and dissolved oxygen in B.C. and Washington waters is not present across the coast-wide dataset, and this allows us to separate the influence of these three variables using correlational SDMs.

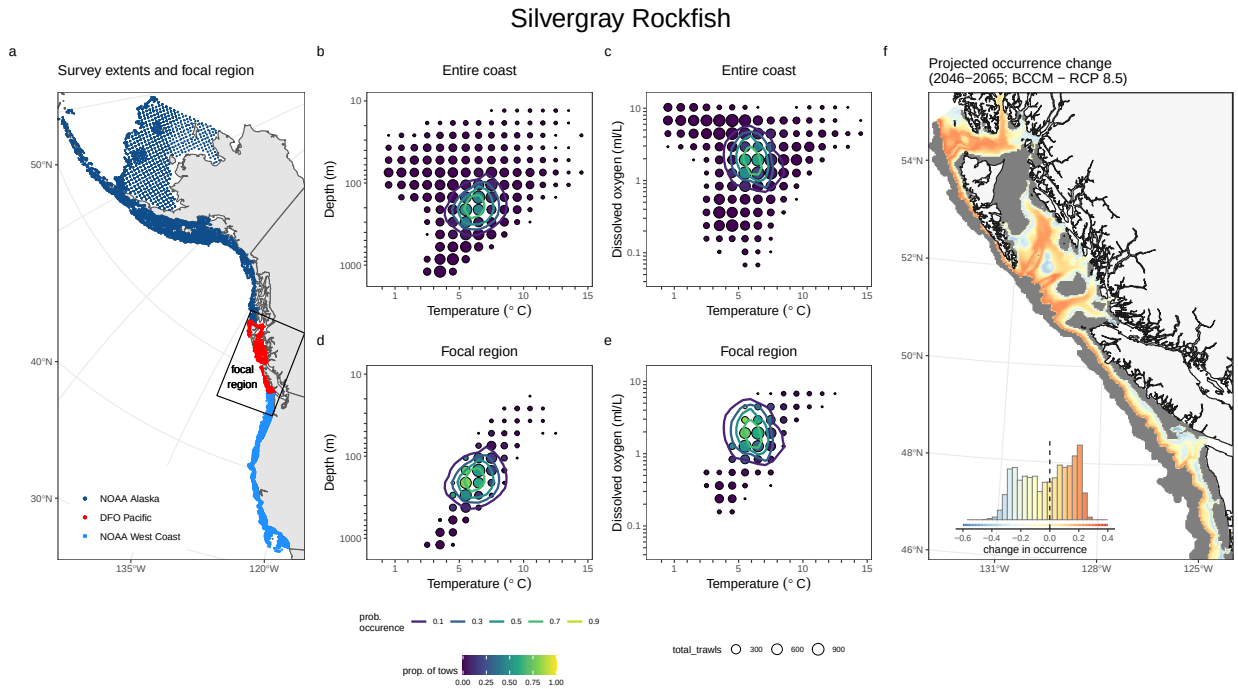

Figure 1: Overview of the SDM fitting and projection process using (Silvergray Rockfish - *Sebastes brevispinis*) as an example. Panel (a) shows the extent of the groundfish survey data, with each point representing a single trawl, coloured by survey. Focal region outlined in panel (a) corresponds to the extent of the regional ocean models that are used for the future projections. Panels c–e show the trawl data binned in environmental space for temperature by depth (b, d) and temperature by dissolved oxygen (c, e). The size of the circle shows the number of tows that fall into that bin, the color shows the proportion of those tows where the species was present. The SDM model fit is shown as contour lines of predicted occurrence. Panels b and c show the full coastwide dataset used to fit the SDMs, panels d and e show only the trawls from B.C. and Washington. Panel f shows the projected change in occurrence for each 3 km^2 grid cell between the historical baseline (1986–2005) and the future projection (2046–2065), here based on the BCCM model and RCP 8.5. The inset histogram in panel (f) shows the distribution of values across all 3 km^2 grid cells and provides a legend for the colours shown on the map. Grid cells where the probability of occurrence was projected to be below 0.1 in both the historical and future time periods periods are shown in grey and are not included in the histogram, as we do not consider these to be important habitat for the species. Plots for all species and projected changes from both climate models and both RCP scenarios are available in Appendix A.

Methods

Estimating species response curves

Fisheries independent trawl data We estimated how the observed distribution of groundfish species is determined by temperature, dissolved oxygen, and seafloor depth using data from 33 637 fisheries independent scientific research trawls. This dataset spans the entire U.S. and Canadian west coast of North America (Figure 1a) and includes both species presence and absence in the trawls. The U.S. portions of the coast are surveyed by the National Oceanic and Atmospheric Administration (NOAA) and include the U.S. West Coast Groundfish Bottom Trawl Survey (0 trawls; NOAA West Coast) and the Alaska Groundfish Bottom Trawl Surveys in the eastern Bering Sea, Aleutian Islands and Gulf of Alaska (0 trawls; NOAA Alaska) (Stauffer 2004; Keller *et al.* 2017). The Canadian portion of the coast is surveyed by Fisheries and Oceans Canada (DFO) with the Groundfish Synoptic Bottom Trawl Surveys (0 trawls; DFO Pacific) (Sinclair *et al.* 2003; Anderson *et al.* 2019). We included data from 2000 to 2019. We included all 89 groundfish species that were present in the overall trawl dataset that did not show obvious breakpoints in occurrence that corresponded with the boundaries of the three surveys. However, our final analysis included only the 40 species (listed in the relevant figures) for which the models had adequate forecasting ability as outlined in the "assessing predictive accuracy" section below.

Temperature, depth, and dissolved oxygen for the observed data were obtained by CTD instrumentation and dissolved oxygen sensors deployed on the headrope of the trawls. Dissolved oxygen was available for 16.8% of the trawls. We filled in missing oxygen data using predictions from a Generalized Linear Mixed Effects Models fit with the sdmTMB package (Anderson *et al.* 2021). Full details of the dissolved oxygen model are provided in the Supplementary Materials. This model was able to predict withheld data with an R^2 of 0.947 (Figure S1).

Species distribution model For each species, we modelled species occurrences in the coastwide trawl dataset using a Generalized Linear Model with a binomial distribution and a logit link function to map the linear predictors to the binary presence-absence data. The fixed effects were temperature, log dissolved oxygen, log depth, and survey. We included quadratic terms for temperature, log dissolved oxygen, and log depth to allow species occurrences to peak at intermediate values (Figure 1b–e). A survey term specifying the data source—NOAA West Coast, NOAA Alaska, or DFO Pacific—was included as a factor to account for differences in survey design and gear.

Assessing predictive accuracy We assessed the forecasting accuracy of the SDM by comparing how well a model fit to only data from 2000–2010 could forecast species' occurrences in trawls within our focal region for the period of 2011–2020. This assessment approximates the approach that we used in our projections (described below) but uses the latter half of our trawl data as testing data in order to estimate how well our models can predict future time periods that were not included in the training data. In particular, this post 2010 period includes the marine heatwave that occurred in the region from late 2013 to 2016 (Cavole *et al.* 2016) and so provides a test of how well the model can predict anomalous conditions without historical precedent. The final set of species included in this manuscript includes only those species that exceeded a threshold Tjur R^2 (Tjur 2009) of 0.2 based on the temporal forecasting accuracy assessment. Note that this temporal blocking of training and testing data was only used for assessing the predictive accuracy of the models, the models used to fit the SDMs that were used to make the projections for the 2045–2065 period (described in subsequent sections) included all trawls in the dataset.

Projecting groundfish biodiversity changes in British Columbia and Washington waters

Regional ocean models We based our groundfish biodiversity change projections on two regional models that downscale climate projections: the British Columbia Continental Margin model (BCCM; Peña *et al.* 2019) and the North-Eastern Pacific Canadian Ocean Ecosystem model (NEP36-CanOE; Holdsworth *et al.* 2021). The BCCM model is an implementation of the Regional Ocean Modeling System (ROMS; Haidvogel

et al. 2008) at a 3 km horizontal resolution. The NEP36 model is an implementation of Nucleus for European Modeling of the Ocean (NEMO) numerical framework 3.6 (Madec 2016) at a variable grid spacing between 1.5 and 2.25 km. Both models used anomalies from the Canadian Earth System Model version 2 (Arora *et al.* 2011) at the open boundaries and the Canadian Regional Climate Model version 4 (CanRCM4; Scinocca *et al.* 2016) for the surface boundary conditions to downscale climate projections.

The BCCM model outputs were interpolated from a curvilinear to a regular 3 km grid using a thin plate spline using the fields (Nychka *et al.* 2017) and raster packages (Hijmans 2022). The NEP36 model outputs were interpolated to the same 3 km grid using a linear interpolation. We used a historical baseline of 1986 to 2005 because these years were present in the historical hindcast of the BCCM as well as the historical climatology of the NEP36. We used projected values from these models for 2046 to 2065 based on RCP 4.5 and 8.5. RCP 4.5 represents a scenario with moderate climate change mitigation and RCP 8.5 represents a no mitigation, worst case scenario (Moss *et al.* 2010; Arora *et al.* 2011; Hausfather & Peters 2020).

We used mean summer (April–September) near-bottom temperature and dissolved oxygen averaged across all years in the historical baseline and future projection periods (Figures S2 - S6). Historical temperatures from both models and dissolved oxygen from the BCCM model were comparable to those observed in the research trawl surveys, but oxygen concentrations from the NEP36 model were consistently high. Therefore, we bias corrected the NEP36 data based on the BCCM hindcast as a common baseline. We elected to use proportional change rather than absolute change for this bias correction to avoid negative projected oxygen concentrations. We did this by calculating the proportional change in oxygen and temperature between the historical and future projections for each 3 km^2 grid cell as: x_f/x_h, where x_f represents the future projected value and x_h represents the historical value (Navarro-Racines *et al.* 2020). We then multiplied these proportional changes by the historical BCCM values to obtain future projections that were bias corrected to the BCCM baseline. We calculated proportional changes in temperature in Kelvin and then converted these back to Celsius to avoid issues of estimating proportional increases for values close to zero.

Species level projections We projected the occurrence of each species in each 3 km^2 grid cell for the historical baseline, as well as for each of the two emissions scenarios in each of the two regional ocean models. Projected occurrence change for each scenario and model was calculated as the historical projected occurrence subtracted from the future projected occurrence for each grid cell (Figure 1f). For each species, we excluded grid cells where the projected probability of occurrences fall below 0.1 in both the historical and future periods, as these are not considered to be important habitat. This allows us to exclude areas where the projected change in occurrence is minimal because conditions are unsuitable in both time periods. Our findings remain qualitatively unchanged when we use a threshold of 0.3 (results not shown).

For each species, we estimated the margin for change in each of the three environmental variables by comparing the conditions in which the species was observed (i.e., present in a trawl) in B.C. and Washington to the maximum (temperature and depth) or minimum (oxygen) conditions at which the species was estimated to be present with at least a probability of 0.1 based on our coastwide SDM. We chose to use upper limits for temperature because temperatures are increasing in both climate projections and so we expect maximum temperature thresholds to be predictive of how species respond. Likewise, we used maximum depth thresholds because we expect that species will shift to deeper waters as conditions warm and so maximum depth thresholds will determine limits to the range shifts. We used minimum oxygen thresholds because oxygen is projected to decrease and so minimum oxygen thresholds will determine if species can persist. To determine each threshold, we used within sample predictions from our fitted SDMs (i.e, predicted occurrences for all trawls in our coastwide training dataset). To ensure that the threshold values were reasonable, we only considered values that were within 50 m of the maximum depth, within 1 °C of the maximum temperature, or within 0.5 ml L^{-1} of the minimum dissolved oxygen concentration where the species was observed in the trawl dataset. We compared these threshold values with the conditions in all trawls in our focal region (i.e., B.C. and Washington) where the species was observed, to obtain a distribution that characterizes the margin for change for that species in the region.

We quantified projection uncertainty due to SDM parameter uncertainty as the average width of the 95% confidence interval for the probability of occurrence. For this we took the average value across all grid cells

where the species was projected to be present with at least a probability of 0.1 in the future scenarios, averaged across both regional ocean models and both emissions scenarios. We quantified regional ocean model uncertainty as the absolute difference in projected occurrence in the future scenarios based on the two regional ocean models, averaged across all grid cells where the species were projected to be present with at least a probability of 0.1, and averaged across both emissions scenarios. We quantified scenario uncertainty as the absolute difference in projected occurrence between RCP 4.5 and 8.5, averaged across all grid cells where the species was projected to be present with at least a probability of 0.1, and averaged across both regional ocean models.

Community level projections Projected species richness for each period, regional ocean model, and scenario was calculated as the summed probability of occurrences across all species. Projected species richness change was then calculated as the historical projected richness subtracted from the future projected richness within each 3 km^2 grid cell. All analyses were conducted in R v.4.0.2 (R Core Team 2021).

Results

Of the 89 species that we assessed for predictive accuracy, 40 had a Tjur R^2 greater than our 0.2 threshold for inclusion. The mean and maximum Tjur R^2 of the species that met this threshold was 0.51 and 0.83 respectively (Figure 2b). Across all species, there was no average change (median = -0.0017) in predictive accuracy when predicting post 2010 data (i.e., out of sample) with the pre 2011 data (i.e., within sample). The largest decrease in predictive accuracy in the post 2011 data was -0.14 and the largest increase in predictive accuracy was 0.35 (Figure S3).

Projected occurrence changes for Washington and B.C. varied considerably across species (Figure 2a). These projections were consistent across the two regional ocean models, although the projected changes based on the NEP36 model tended to be slightly larger compared to those based on the BCCM model (Figure 2a). Likewise, the projected changes in species occurrences were similar in models based on the RCP 4.5 and 8.5 emissions scenarios, with RCP 8.5 resulting in projected changes that were of slightly greater magnitude (Figure 2 vs. S7). Under the RCP 8.5 scenario with the BCCM (NEP36) model, 5 (6) species were projected to decrease in occurrence in at least 95% of the region where they were estimated to be present, 6 (7) species were projected to increase in occurrence in at least 95% of the region where they were estimated to be present, while the remaining 29 (27) species were projected to increase and decrease in prevalence in different parts of the region. The projections were similar for the RCP 4.5 scenario with 7 (6) species decreasing in occurrence, 6 (7) species increasing in occurrence, and 27 (27) showing variable changes in projected occurrence.

Quantifiable uncertainty in the probability of occurrence change varied across species, ranging from 0.077 for Sandpaper Skate to 0.357 for Deepsea Sole, with an average of 0.163 across all species (Figure 2c). Uncertainty in projected occurrences as the result of SDM model parameter uncertainty resulted in the greatest variation in projected occurrences, with the average 95% confidence interval width across all grid cells (with a projected occurrence > 0.1) and species of 0.08. The next greatest source of uncertainty was due to variation in projected occurrences across the two regional ocean models, which had an average difference of 0.059 across all grid cells (with a projected occurrence > 0.1) and species. Emission scenario differences contributed the least uncertainty to our projections, with an averaged difference of 0.024 across all grid cells (with a projected occurrence > 0.1) and species.

There was considerable variation in how far species in B.C. and Washington waters are from our estimated maximum temperature thresholds (Figure 3a). Some species such as Greenstriped Rockfish and Stripetail Rockfish were more than 5 °C away from their estimated temperature thresholds, while others such as Shortraker Rockfish and Sand Sole were found at temperatures right up to their threshold. In contrast, groundfish in B.C. and Washington tended to extend all the way to their estimated maximum depth thresholds and their minimum oxygen thresholds (Figure 3b, c). In general, the species that were projected to increase in occurrence throughout B.C. and Washington are those that were far from their temperature thresholds (Figure 3a). Species that were projected to have mixed responses under future conditions were those that have wide depth ranges (Figure 3b). Species that were projected to decrease in occurrence throughout the

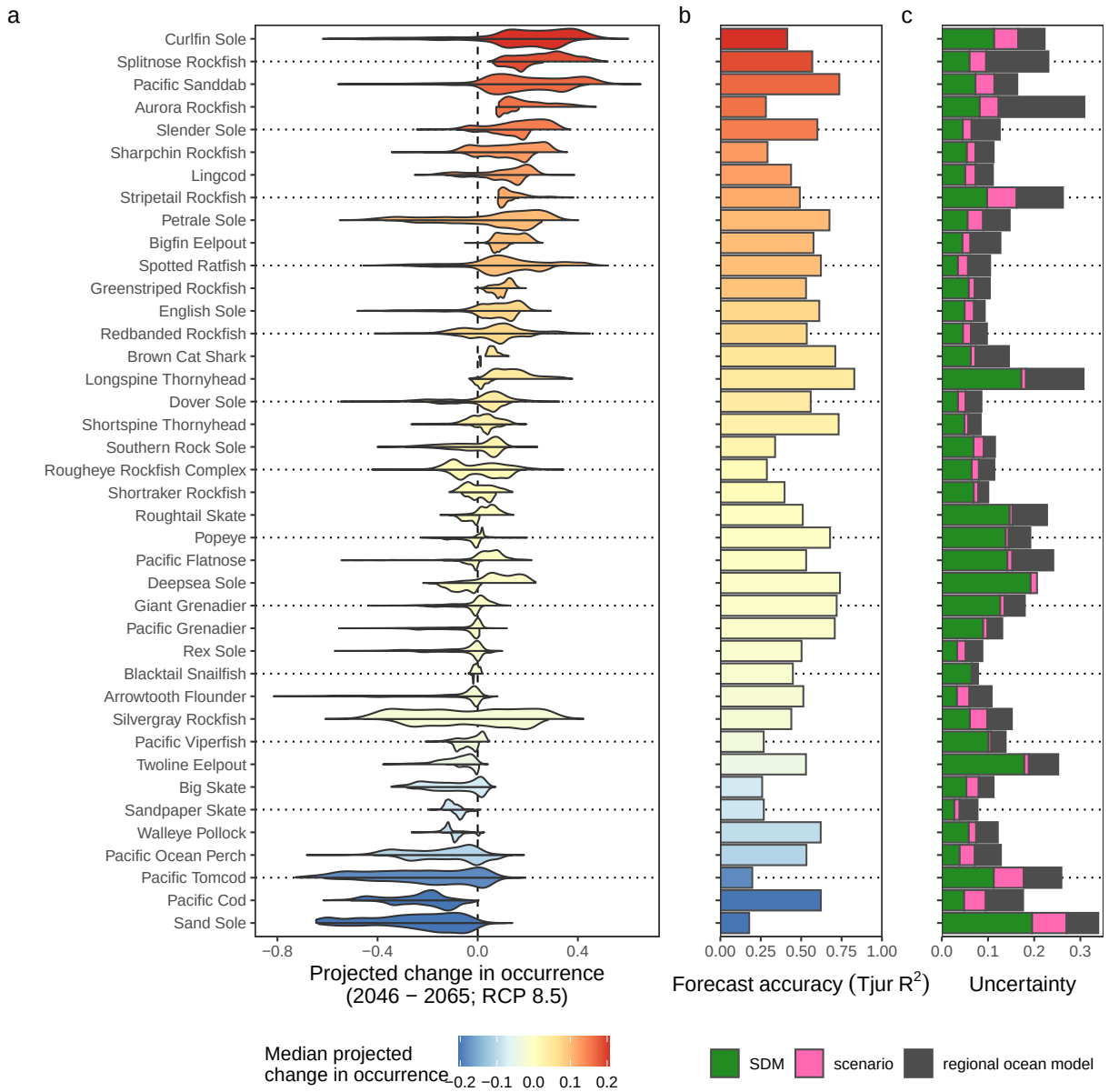

Figure 2: Distributions of projected change in occurrences across the 3 km^2 grid cells in the study region for all species (a) based on a comparison of average conditions in 1986–2005 vs 2046–2065 under the RCP 8.5 emissions scenario (see Figure S7 for RCP 4.5). For each species, the upper half of the distribution shows projections based on the NEP36 model and the lower half shows projections based on the BCCM model. Grid cells where projected occurrences fall below 0.1 in both the historical and future periods are not considered to be habitat and changes in occurrence in these grid cells are excluded from the distributions. Species are ordered from most positive to most negative median change in projected occurrence. Panel (b) shows the forecast accuracy, measured as Tjur R^2 for post 2010 data in the focal region using a model trained on all pre 2011 data. The color indicates the median projected change in occurrence across all 3 km^2 grid cells in the region based on the BCCM RCP 8.5 scenario. Panel (c) shows the average estimated uncertainty of the projections across all 3 km^2 grid cells where the probability of occurrence is greater than 0.1 in both the historical and future periods, separated by SDM uncertainty (95% confidence interval), emmissions scenario (difference), and regional ocean model difference.

region are those that were close to their maximum temperature thresholds and which occupy a relatively narrow range of depths.

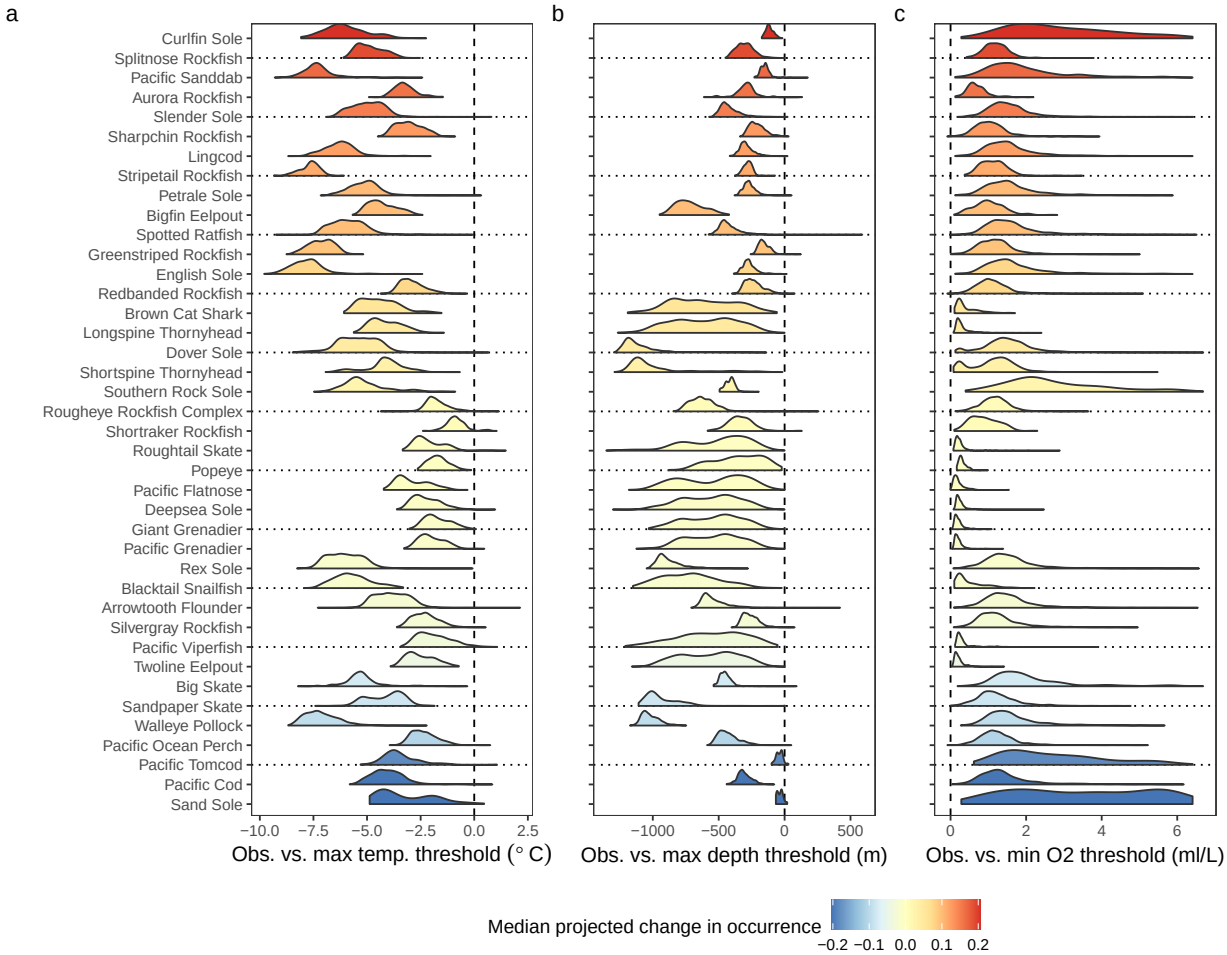

Figure 3: Species' margin for change in temperature (a), depth (b), and dissolved oxygen (c). Margins are calculated as the observed environmental value in each trawl where a species was present minus the threshold value for that variable, beyond which occurrence is estimated to fall below 0.1 based on the SDM. Threshold values are for high temperature and depth and for low dissolved oxygen concentrations. Distributions represent the margins for all trawls where a species was present. The distance between the distribution and the dashed 0 line (left for temperature and depth, right for oxygen) indicates the degree to which the species is estimated to be able to tolerate warmer, deeper, or lower oxygen conditions respectively. As for Figure 2, the color indicates the median projected change in occurrence between 1986–2005 vs 2046–2065 for the RCP 8.5 scenario in the BCCM model across all 3 km^2 grid cells in the region and species are ordered from most positive to most negative change.

Projected species richness changes varied spatially across our focal region, ranging from -3.9 to 2.6, with a median of 0 across both regional ocean models and both emmissions scenarios (Figures 4, S8 - S10). The pattern of projected change was largely consistent across the two regional ocean models, but the magnitude of projected change was slightly larger for projections based on the NEP36 model (Figure 4a vs. S9a). Projected species richness change based on the two regional ocean models did differ in the deepest waters, where changes were more variable and more positive based on the NEP36 model. Projected richness changes were similar but of lesser magnitude for the RCP 4.5 emissions scenarios (Figures S8 and S10). These changes varied by depth, with decreases projected at depths shallower than 100 m, increases occurring between 100 m

and 600 m, and no change or minor decreases projected for depths greater than 600 m (Figure 4c). Decreases in species richness at the shallowest depths were associated with waters where warming is projected to be greatest (Figure 4c, d). At mid-depths, the largest species richness increases were projected at around 300 m, below which future oxygen is projected to be 2 mL L^{-1} or lower in B.C. and Washington under the RCP 8.5 scenario.

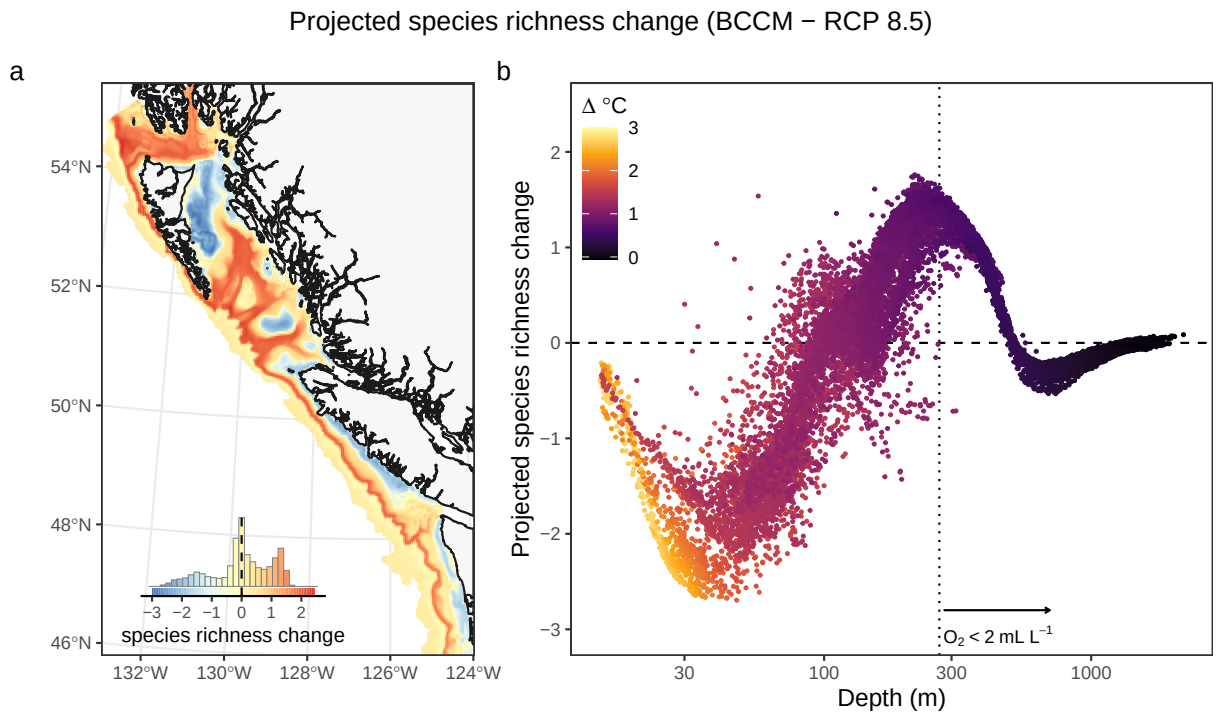

Figure 4: Projected species richness change (a) mapped across the study region between historical (1986–2005) and future (2046–2065, RCP 8.5) projected environmental conditions based on the BCCM model (see the supplement materials for results for the NEP36 model and for RCP 4.5). The inset histograms in panel (a) shows the distribution of values across all 3 km^2 grid cells and provides a legend for the colours shown on the map. Panel (b) shows projected species richness change in each 3 km^2 grid cell as a function of seafloor depth colored by projected temperature change. The vertical dashed line in panel b shows the depth at which the average oxygen concerntation falls below 2 ml L^{-1} and the arrow indicates that oxygen levels decrease further with depth.

Discussion

Our analysis suggests that projected warming and deoxygenation is likely to cause a reorganization of the groundfish community in B.C. and Washington by 2046 to 2065. We estimate that species will differ in their responses to climate change; some species will benefit from warmer conditions and increase in occurrence, others will move to greater depths as conditions warm, but those that cannot tolerate deeper depths or lower oxygen are expected to decrease in occurrence. While species that are projected to decline are roughly balanced by species that are projected to increase, the overall impact on the community is expected to depend on depth. At depths of less than 100 m where warming is projected to be greatest, we expect to see a decline in species richness. At mid depths between 100 and 600 m we expect species richness to increase as shallow species shift to deeper depths and species that live at these mid depths benefit from the warmer conditions. The increase in species richness is projected to be greatest at depths around 300 m as below this hypoxic conditions (i.e., < 2 mL L^{-1}; Diaz & Rosenberg 2008) may prevent further species range shifts. At depths below 600 m warming is projected to be minimal, and the community is expected to

remain relatively unchanged, with species richness either decreasing slightly as the result of deoxygenation or remaining stable. While the magnitude of these projected changes to the groundfish community varies depending on the regional ocean model used and the emissions scenario, the overall pattern of change is consistent in all cases. This result suggests that our expectations for how the groundfish community will reorganize should be qualitatively robust to uncertainty in how climate change will play out over the coming decades.

These findings demonstrate the importance of accounting for the influence of depth and dissolved oxygen when projecting how climate change will affect species in marine environments. Based on our projections, it is not possible to determine how a species will respond to warming based only on its temperature response curve because species vary in the degree to which their tolerance to depth and low oxygen constrain their ability to shift to deeper depths as conditions warm (Figure 3). Therefore, SDMs which do not account for depth and dissolved oxygen (e.g., Morley *et al.* 2018) may underestimate the sensitivity of marine organisms to climate change because they assume that species can always shift to deeper waters when conditions warm. In contrast, models that rely only on sea surface temperatures (e.g., García Molinos *et al.* 2016) assume that species cannot shift in depth to deal with warming, thus they are likely to overestimate the sensitivity of groundfish to climate change.

Of course, additional variables that we have not accounted for may further constrain species distributions as well as their responses to warming and oxygenation. For example, projected ocean acidification (Peña *et al.* 2019; Holdsworth *et al.* 2021) may impact fish populations (Branch *et al.* 2013; Haigh *et al.* 2015), but SDMs are not well suited to projecting these because we lack occurrence data across relevant pH ranges. Species distributions may also be constrained to certain seafloor substrate types (Pirtle *et al.* 2019) and including substrate in our models may result in more accurate projections (e.g., Morley *et al.* 2018). However, the lack of comprehensive substrate data for the entire extent of the groundfish surveys used in our analysis precluded us from including this variable in our models. It is likely that the inclusion of additional variables would have improved model performance, and may have increased the number of species that met our inclusion criteria based on the temporal forecasting assessment. However, many of the unobserved variables also change with depth so, as implemented here, depth may be a proxy for these processes. A previous study of groundfish in B.C. estimated that the addition of oceanographic variables, including substrate, currents, and primary production, to a model that already included depth only resulted in a minor increase in the accuracy of predictions (Thompson *et al.* 2022).

By combining spatially extensive scientific survey data with regional ocean models, we were able to develop robust models that are informed by broad spatial and environmental gradients but make projections at a relatively high resolution. If we had trained our SDMs on data only from our focal region we would not be including the full range of environmental conditions that define the distributions of these species. Furthermore, the high correlation between depth, temperature, and oxygen in B.C. and Washington would have prevented us from distinguishing their unique influence on species' distributions (Thompson *et al.* 2022). While some species in our models have ranges that extend beyond the broad spatial extent of the surveys, we expect that this had negligible impact on our projections because our focal region is situated in the middle of the geographic and environmental space sampled by the surveys. Reassuringly, the future environmental conditions that are projected by our regional models fall within the range of conditions present in our survey data, except in the few warmest grid cells where future conditions are projected to exceed our observational range by less than a degree Celsius (Figure S4). Thus, we are largely avoiding extrapolating into novel climate conditions, which is a key source of uncertainty in many SDM projections (Veloz *et al.* 2012). In contrast, if we had extended our projections to cover the full spatial extent of the survey data we would have had to use low resolution outputs from global climate models, which have not been downscaled to incorporate the complex bathymetry of the continental shelf (Hewitson & Crane 1996; Giorgi *et al.* 2009). Alternatively, we could have stitched together multiple regional ocean models (e.g., Veneziani *et al.* 2009; Hermann *et al.* 2019; Kearney *et al.* 2020) but this would have required additional assumptions because models differ in their underlying mechanics, data, and assumptions. As our goal was to make projections that could be used for ongoing management initiatives in Canadian Pacific waters, this approach was not necessary.

Projecting biodiversity responses to climate change involves considerable uncertainty (Urban *et al.* 2016)

and our approach allows us to quantify some aspects of this. Of the uncertainty that we could quantify, roughly half was due to uncertainty in the parameters in our SDMs and the remainder was due to regional ocean model uncertainty or scenario uncertainty. To reduce the influence of internal variability in climate, we use 20–year climatologies with a future period that is far enough in the future to ensure that changes are unambiguously due to greenhouse gases (Hawkins & Sutton 2009; Holdsworth *et al.* 2021). We have made projections based on two different emissions scenarios, and two different regional ocean models that are both downscaled from the same global model, the second generation Canadian Earth System model (CanESM2), using different downscaling techniques. While the BCCM model was run inter-annually and then averaged to produce the climatologies (Peña *et al.* 2019), the NEP36 model used atmospheric climatologies with augmented winds to force the ocean model and produce representative climatologies (Holdsworth *et al.* 2021). Comparing these regional projections provides an estimate of the uncertainty across different regional downscaling models and methods. We find that the projected impacts of climate change on the groundfish community are more sensitive to the differences in the regional ocean models than they are to the emissions scenarios used. However, these differences are in magnitude (changes tend to be larger based on NEP36 compared to the BCCM) rather than in direction, with both models resulting in similar overall patterns of biodiversity change and turnover for the groundfish community. Over the sixty year time period (1986–2005 vs. 2046–2065) used in our study, our projections suggest that groundfish community changes are similar regardless of the scenario used which is not surprising given the fact that the two emissions scenarios do not appreciably differ until later in the 21st century (Arora *et al.* 2011). Ideally, we would also quantify uncertainty due to differences between global climate models and use the ensembles from each of the models (e.g., Frölicher *et al.* 2016; Morley *et al.* 2018), however, regional models driven by other global models have not yet been developed for this region. We expect that projections based on different global climate models would show greater variation than we see between our regional ocean models, but they would produce similar overall patterns in projected groundfish community change.

One aspect of projection uncertainty that we cannot quantify is that which is due to eco-evolutionary processes (Urban *et al.* 2016). Interactions between species, movement across the seafloor (e.g., dispersal, migration, foraging Guzman *et al.* 2019), and evolution all influence current species distributions as well as the way that species will respond when conditions change (Urban *et al.* 2012; Norberg *et al.* 2012; Thompson & Fronhofer 2019). For example, our projections suggest that many species will shift to deeper depths as conditions change. However, this assumes that prey exist in sufficient abundance at those new depths, and that the species will be able to establish in the face of novel competitors and predators (Gilman *et al.* 2010). This also assumes that species cannot adapt or acclimate in areas where they are projected to decrease in occurrence (Aitken *et al.* 2008). Thus, our projections are most uncertain for areas where habitat is projected to transition from suitable to unsuitable or vice versa. Conversely, eco-evolutionary processes should result in less uncertainty in areas that are projected to remain as suitable habitat for a species. These areas that are projected to remain suitable offer a "no regrets" conservation opportunity as their protection is likely to benefit the species, both now and in the future.

The species in our analysis are all under some degree of fishing pressure—either as the target of fisheries or as bycatch (Anderson *et al.* 2019). Climate change will make the management of these species more challenging and is likely to threaten the sustainability of some fisheries (Duplisea *et al.* 2021). Estimated species' sensitivity to climate change is a key knowledge gap in current groundfish stock assessments in this region. While changes in biomass are likely to differ from the changes in occurrence that we have projected here (Thompson *et al.* 2022), we expect occurrence changes to be informative of the sensitivity of species to climate change. Thus, our results can be used to integrate climate change risk into stock assessments and ecosystem-based fisheries management in this region (Duplisea *et al.* 2021; Roux *et al.* 2022). For many species, this may require accounting for climate driven shifts in species distributions and biomass across international boundaries (Palacios-Abrantes *et al.* 2022).

With this analysis, we have demonstrated how spatially extensive scientific survey data can be combined with high resolution regional ocean models to provide projections of groundfish community changes at a scale that is relevant to developing spatial management strategies to preserve marine biodiversity and sustainable fisheries. Furthermore, we have demonstrated that our overall projected patterns of biodiversity change are consistent regardless of the level of emissions, and across the two different regional ocean models that are available for our region. However, had we chosen a more distant future time period, the sensitivity to

emission scenario would have been greater. These projections can inform ongoing management initiatives to ensure that they account for anticipated impacts of climate change. For example, Canada is in the process of establishing a network of marine protected areas (MPAs) and refuges to provide long-term conservation of biodiversity (Environment and Climate Change Canada 2021). While climate change adaptation principles are largely lacking from Canadian MPA management plans to date (O'Regan *et al.* 2021), our projections offer an opportunity to ensure that new protected areas in B.C. are situated in areas that will benefit groundfish and other species, both now and under future climates.

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Supplemental Methods

Dissolved Oxygen Model

We opted to use a phenomenological model of dissolved oxygen rather than use values from an oceanographic model because we could not find an oceanographic model that spanned the entire spatial extent of the trawl dataset at a sufficient spatial resolution to match to the missing observations. Instead, we estimated the missing oxygen observations using a Generalized Linear Mixed Effects Models fit with the sdmTMB package (Anderson *et al.* 2022). This model predicted oxygen as a function of near bottom log pressure, temperature, exponential potential density (σ_θ) and month. A spatiotemporal random field was also used to capture spatiotemporal variation that was not associated with these fixed effects (details below). Potential density (σ_θ) was calculated from salinity and temperature values using the gsw R package (Kelley *et al.* 2021) with a reference pressure of 0 dbar. Near bottom measurements of salinity, temperature and pressure were sourced from ocean profile data that were collected during trawl and longline fisheries surveys along the Canadian and US west coasts. Data were sourced from the International Pacific Halibut Commission (IPHC) ocean profile data (Sadorus *et al.* 2016) from 2009 to 2015 and all groundfish trawls where oxygen was measured. This resulted in a final dataset of 12581 observations.

We modelled log dissolved oxygen using a Gaussian observation model:

$$\begin{aligned}
&O_{s,t} = \text{Normal}(\mu_{s,t}, \sigma^2),\\
&\mu_{s,t} = \boldsymbol{X}_{s,t}\boldsymbol{\beta} + \omega_s + \delta_{s,t},\\
&\boldsymbol{\omega} \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma_\omega}),\\
&\boldsymbol{\delta}_{t=1} \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma_\epsilon}),\\
&\boldsymbol{\delta}_{t>1} = \rho\boldsymbol{\delta}_{t-1} + \sqrt{1-\rho^2}\epsilon_t, \epsilon_t \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma_\epsilon}),
\end{aligned} \tag{S.1}$$

where $O_{s,t}$ is log dissolved oxygen at location s in year t, μ represents the mean, and σ represents the observation error standard deviation. The parameter $X_{s,t}$ represents the vector of predictors (temperature, pressure, potential density, month) and β represents the corresponding vector of coefficients. The parameter ω_s represents the spatial random effects. These were assumed to be drawn from Gaussian Markov random fields with a covariance matrix Σ_ω that was constrained by Matérn covariance functions (Cressie & Wikle 2011). The parameter ϵ_s represents the spatiotemporal random effect, which follows an autoregressive (AR1) process with first-order correlation ρ. Oxygen solubility is influenced by temperature and pressure and a non-linear correlation between dissolved oxygen concentration and potential density has been documented in this region (Stefánsson & Richards 1964). Thus we included each of these variables as predictors using plate regression splines. Dissolved oxygen is also understood to fluctuate over the course of the year and so we included month as a predictor using a cyclic cubic spline. The spatial component of the random fields was modelled using a triangulated mesh with vertices selected based on a maximum distance threshold of 15km cut off. We trained the dissolved oxygen model on 70% of the observations and tested it on the remaining 30% hold out data.

Supplemental Figures

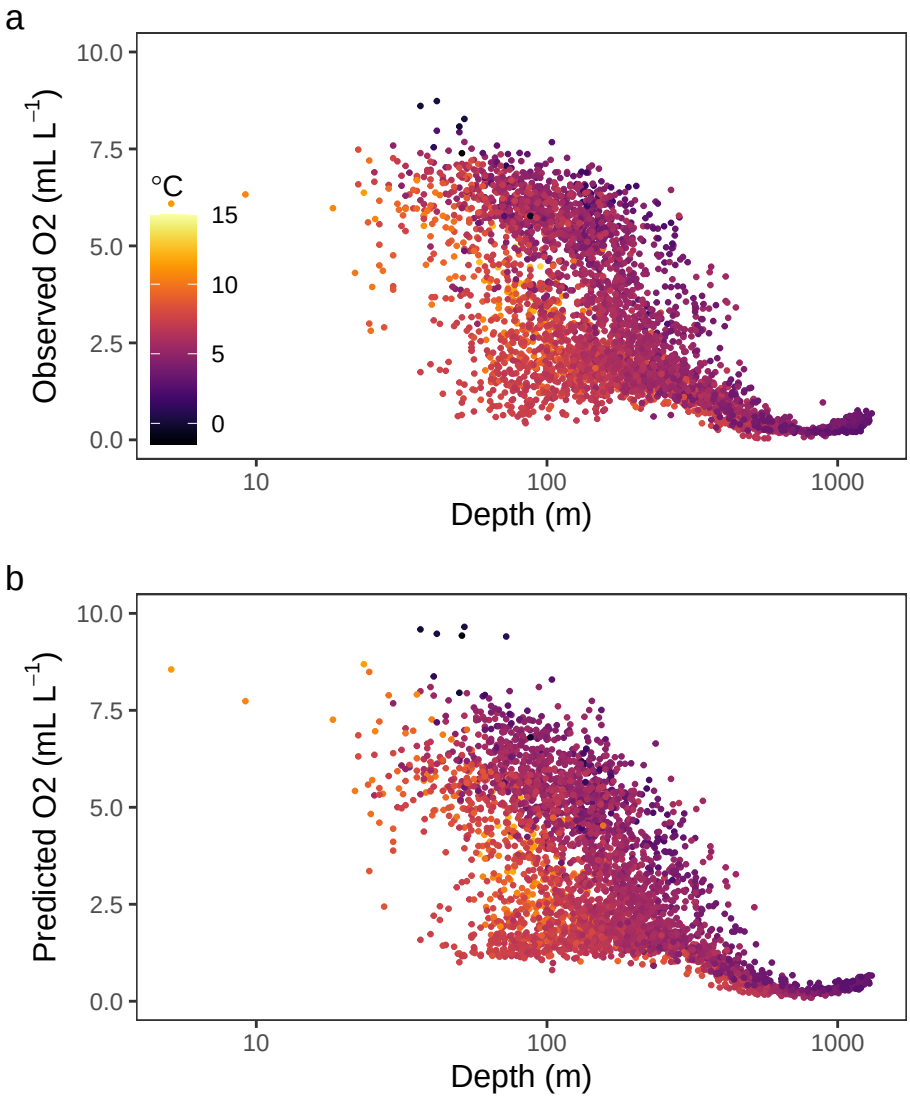

Figure S1: Observed (a) and predicted (b) dissolved oxygen as a function of depth in data withheld from the model.

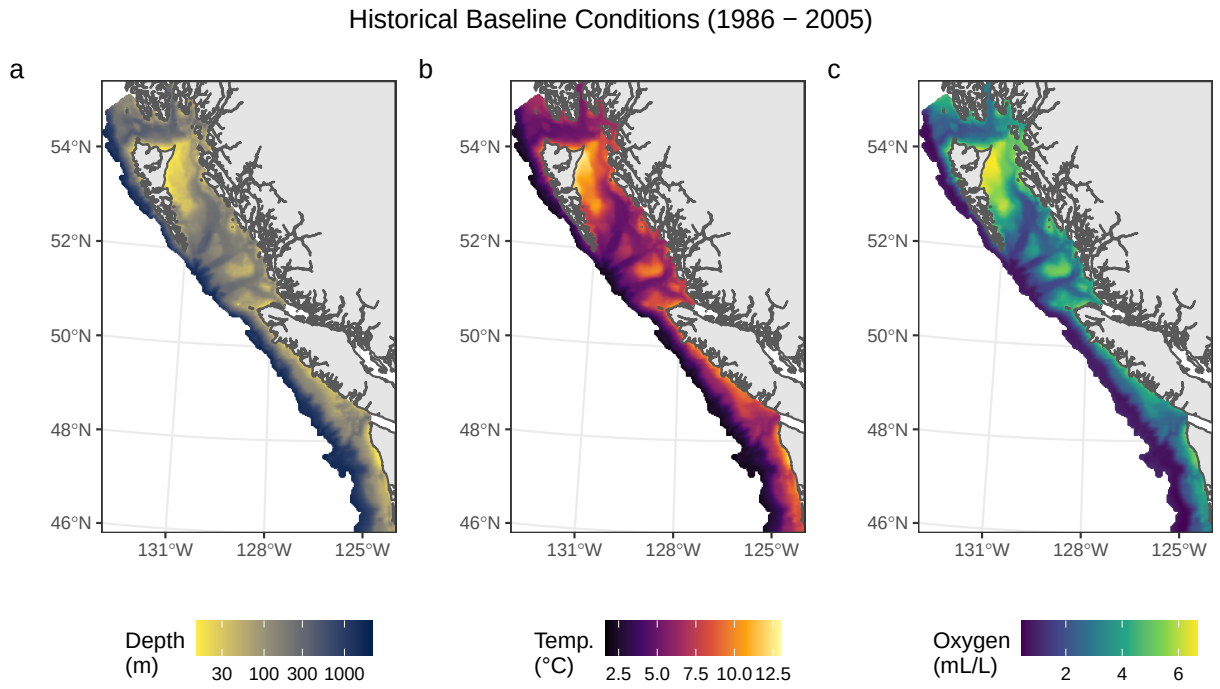

Figure S2: Maps of the historical baseline conditions (1986 - 2005) for seafloor depth (a), near seafloor temperature (b) and near seafloor dissolved oxygen (c).

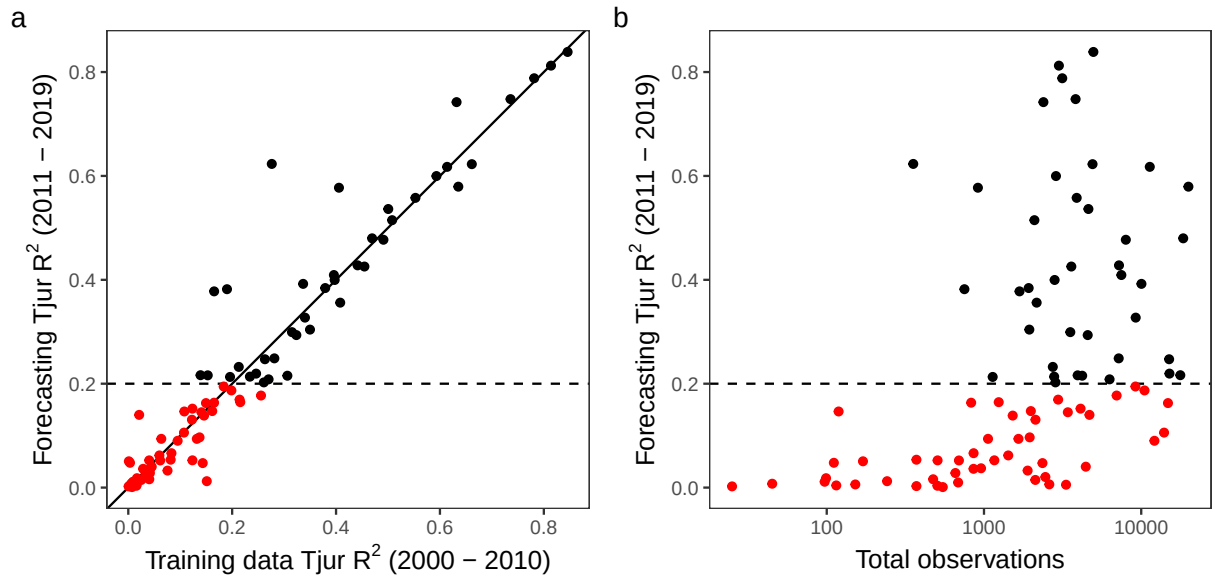

Figure S3: Model accuracy assessment showing the Tjur R^2 for each species for predictions made for post 2010 data (i.e., forecasting) compared to pre 2011 (i.e., training data) research trawl data from B.C. and Washington (a) or the total number of observations across all surveys (b). The horizontal dashed line shows the 0.2 Tjur R^2 cut off for inclusion in the analysis. Species that meet this threshold are shown in black, species that do not are shown in red.

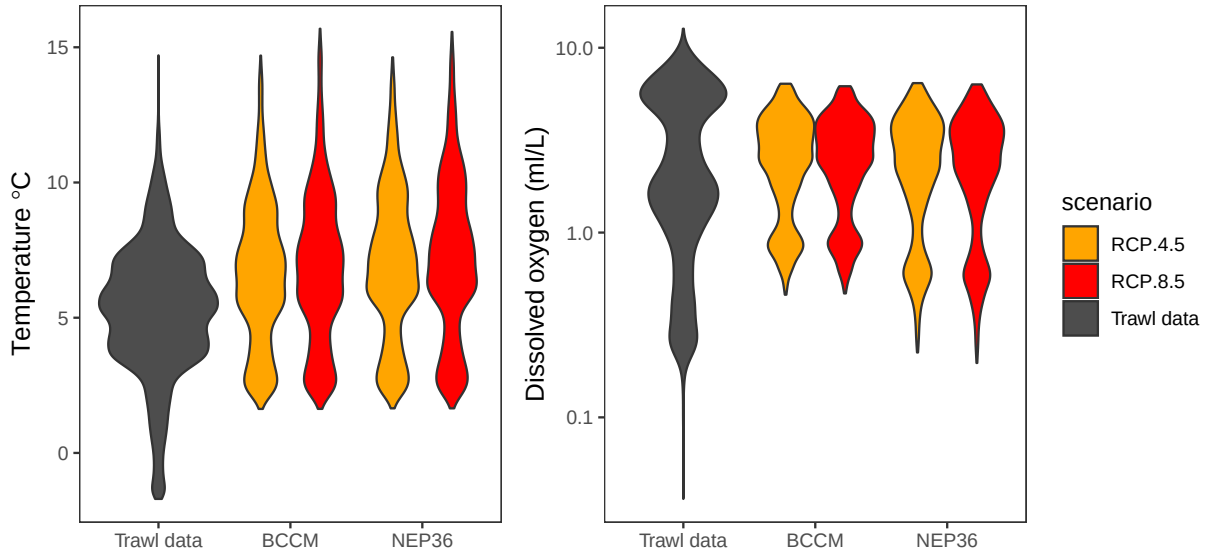

Figure S4: Comparison of the distribution of temperature (a) and dissolved oxygen (b) in the full trawl dataset and the future projected conditions in the two regional ocean models and RCP scenarios.

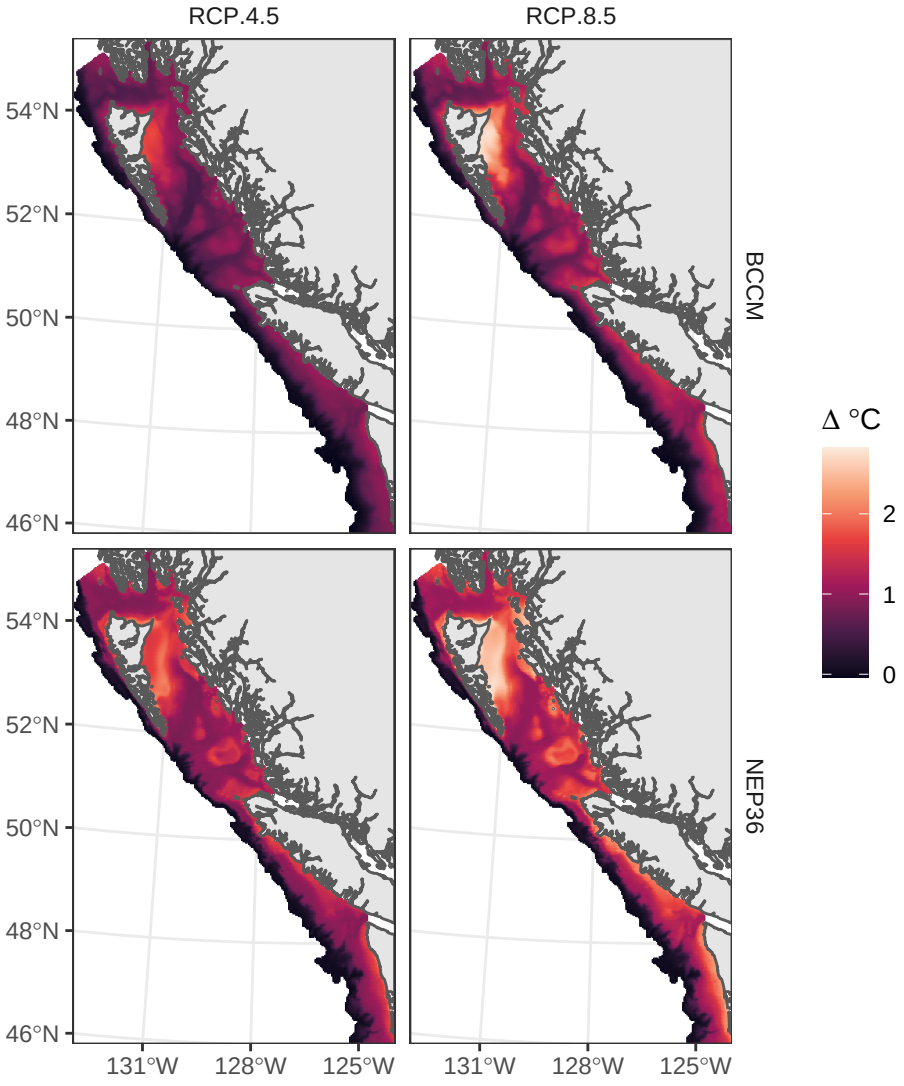

Figure S5: Maps of near seafloor temperature change in the two regional ocean models (rows) and the two RCP scenarios (columns) from the 1986–2006 baseline to 2046–2065.

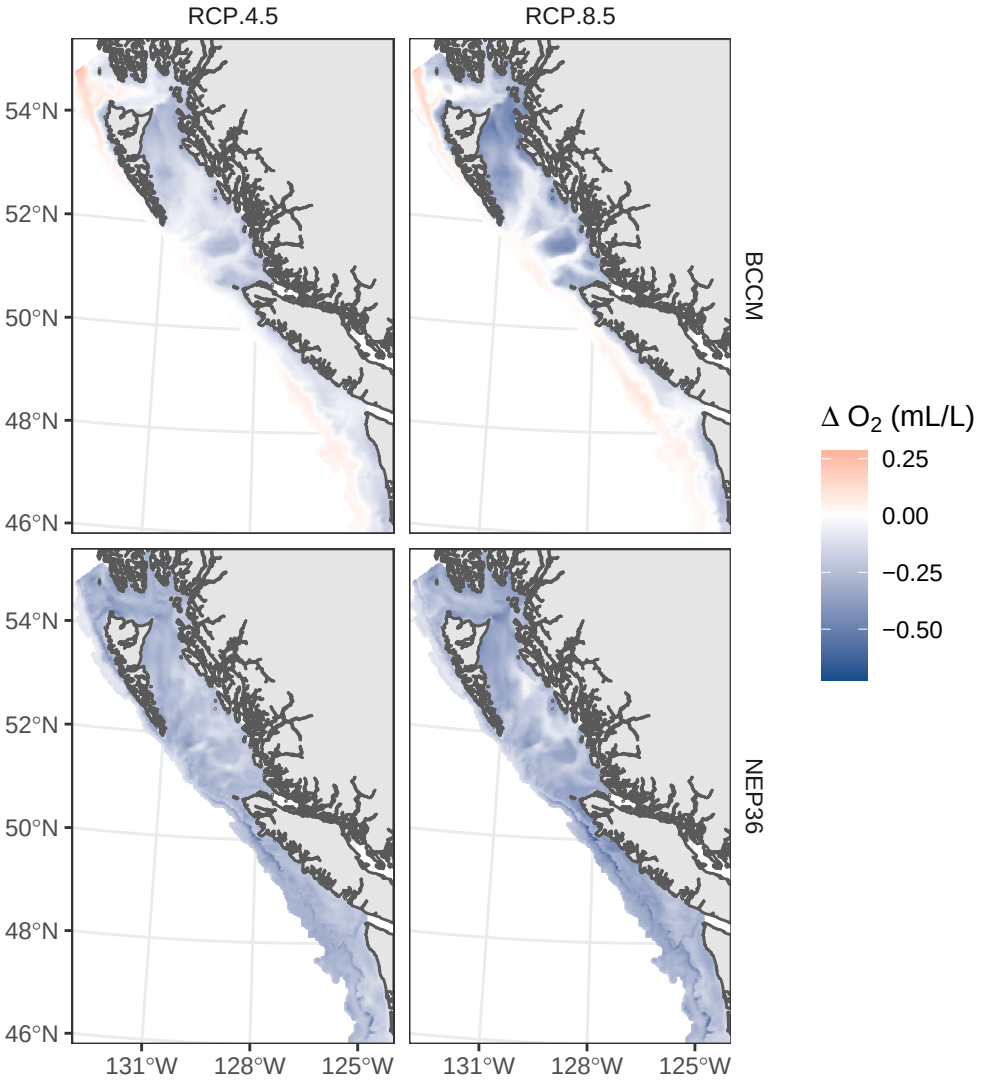

Figure S6: Maps of near seafloor oxygen change in the two regional ocean models (rows) and the two RCP scenarios (columns) from the 1986–2006 baseline to 2046–2065.

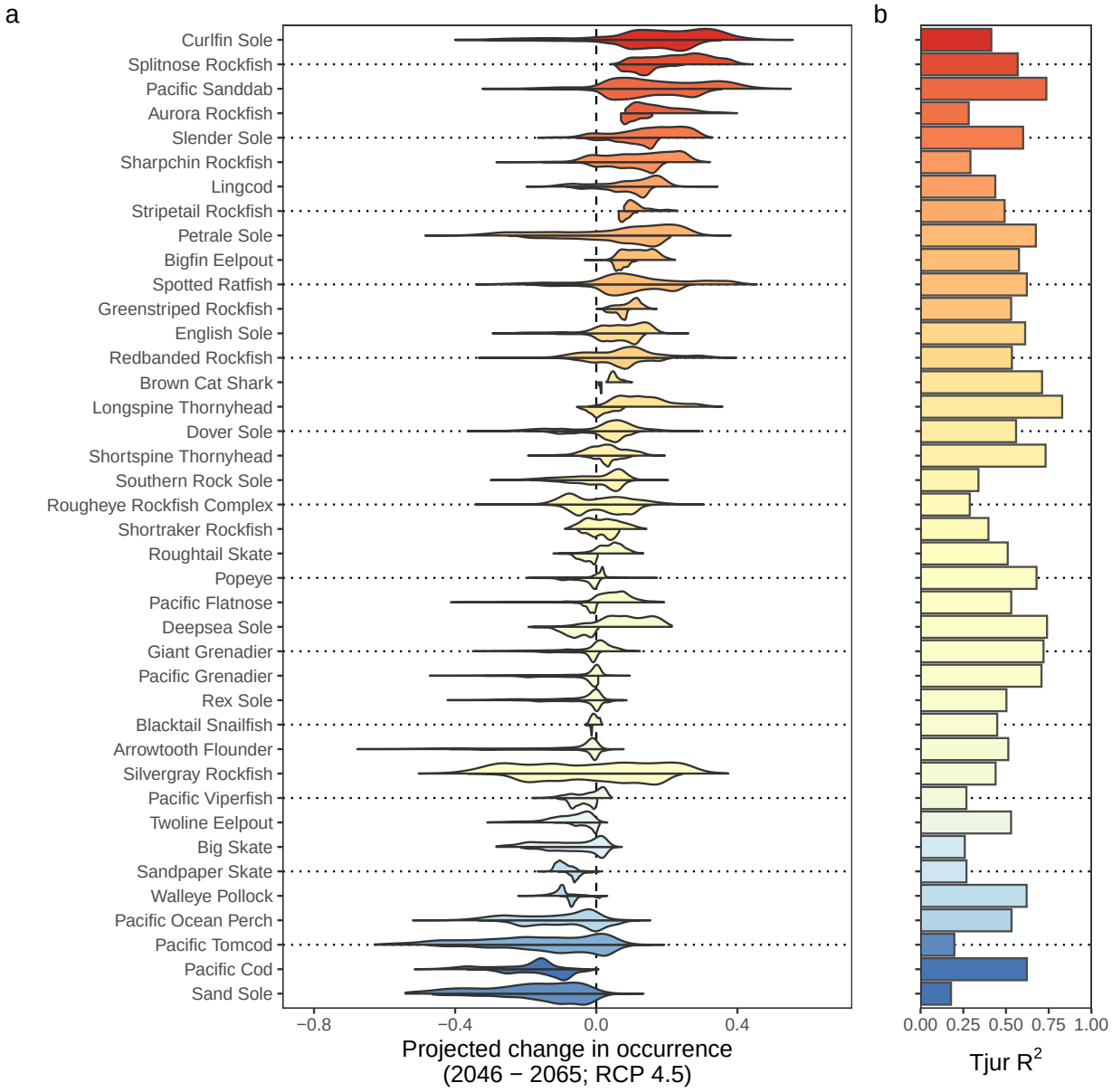

Figure S7: Distributions of projected change in occurrences across the 3 km^2 grid cells in the study region for all species (a) based on a comparison of average conditions in 1986–2005 vs 2046–2065 under the RCP 4.5 emissions scenario. For each species, the upper half of the distribution shows projections based on the NEP36 model and the lower half shows projections based on the BCCM. Grid cells where projected occurrences fall below 0.1 in both the historical and future periods are not considered to be core habitat and changes in occurrence in these grid cells are excluded from the distributions. Panel (b) shows the Tjur R^2 predictive power based on the temporal forecasting assessment. The color indicates the median projected change in occurrence across all 3 km^2 grid cells in the region based on the BCCM RCP 4.5 scenario. Species are ordered from most positive to most negative change.

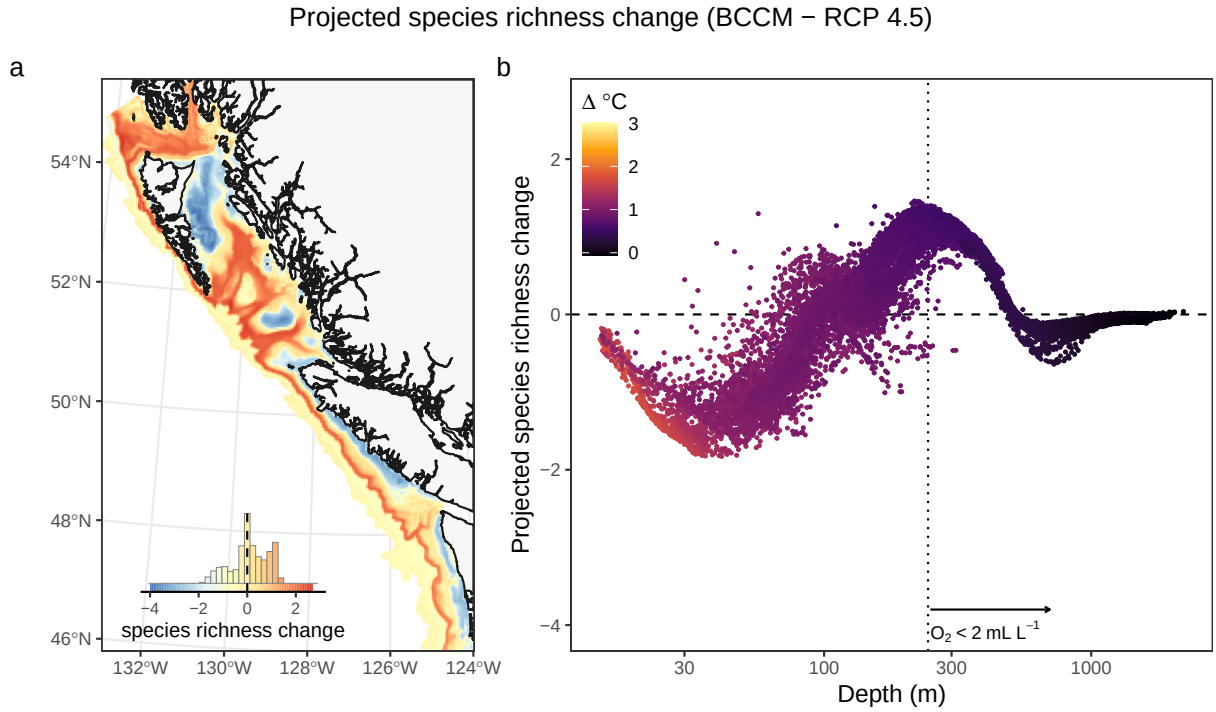

Figure S8: Projected species richness change (a) mapped across the study region between historical (1986–2005) and future (2046–2065, RCP 4.5) projected environmental conditions based on the BCCM model. The inset histograms in panels (a) shows the distribution of values across all 3 km^2 grid cells and provides a legend for the colours shown on the map. Panel (b) shows projected species richness change in each 3 km^2 grid cell as a function of seafloor depth colored by projected temperature change. The vertical dashed line in panel b shows the depth at which the average oxygen concerntation falls below 2 ml L^{-1} and the arrow indicates that oxygen levels decrease further with depth.

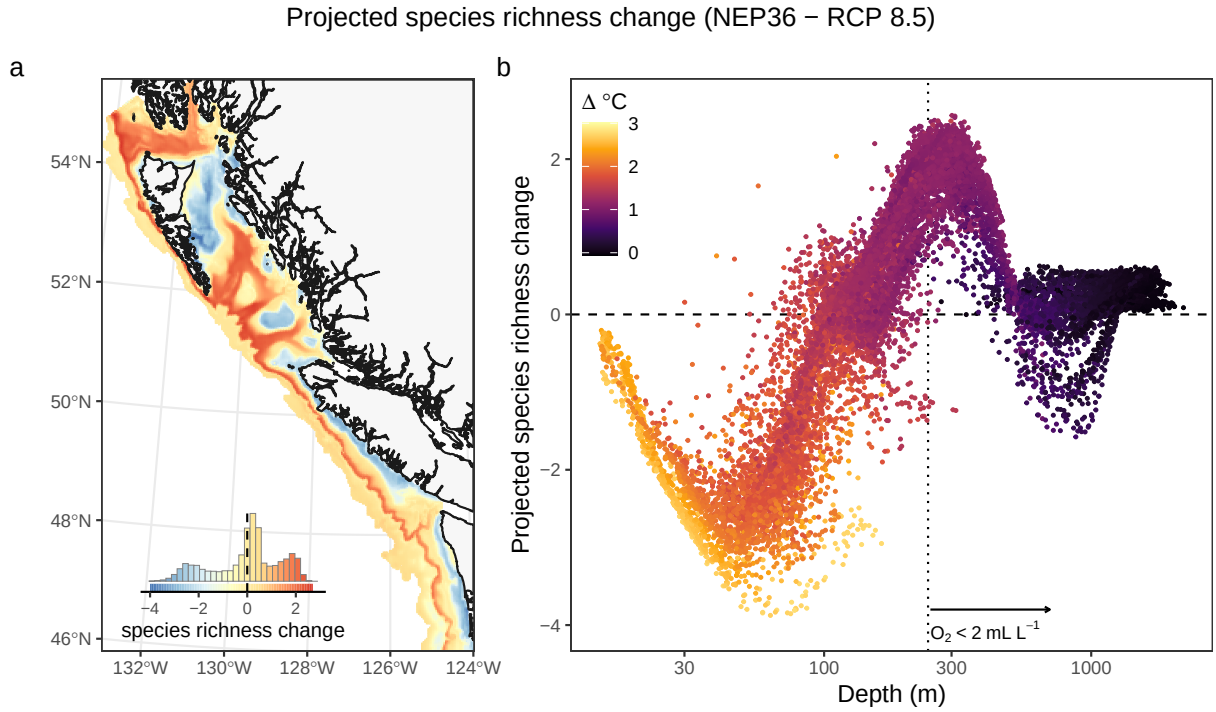

Figure S9: Projected species richness change (a) mapped across the study region between historical (1986–2005) and future (2046–2065, RCP 8.5) projected environmental conditions based on the NEP36 model. The inset histograms in panels (a) shows the distribution of values across all 3 km^2 grid cells and provides a legend for the colours shown on the map. Panel (b) shows projected species richness change in each 3 km^2 grid cell as a function of seafloor depth colored by projected temperature change. The vertical dashed line in panel b shows the depth at which the average oxygen concerntation falls below 2 ml L^{-1} and the arrow indicates that oxygen levels decrease further with depth.

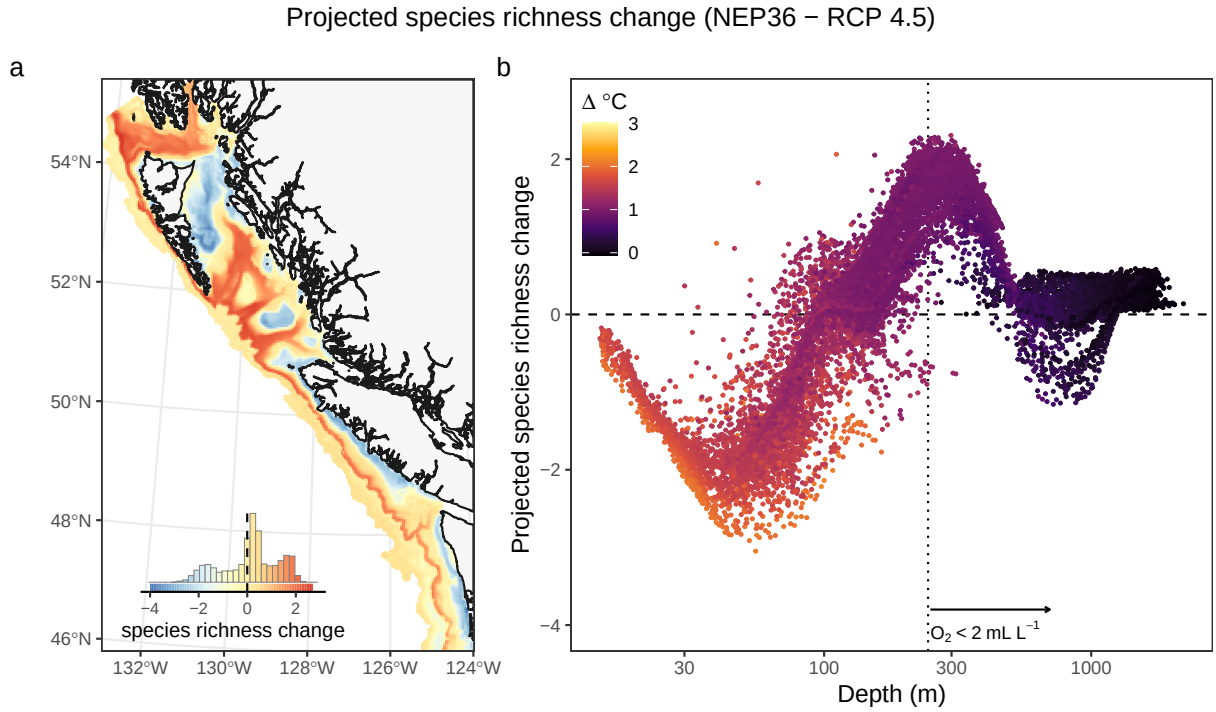

Figure S10: Projected species richness change (a) mapped across the study region between historical (1986–2005) and future (2046–2065, RCP 4.5) projected environmental conditions based on the NEP36 model. The inset histograms in panels (a) shows the distribution of values across all 3 km^2 grid cells and provides a legend for the colours shown on the map. Panel (b) shows projected species richness change in each 3 km^2 grid cell as a function of seafloor depth colored by projected temperature change. The vertical dashed line in panel b shows the depth at which the average oxygen concerntation falls below 2 ml L^{-1} and the arrow indicates that oxygen levels decrease further with depth.