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APPLIED ECOLOGY

Species redistribution creates unequal outcomes for multispecies fisheries under projected climate change

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Climate change drives species distribution shifts, affecting the availability of resources people rely upon for food and livelihoods. These impacts are complex, manifest at local scales, and have diverse effects across multiple species. However, for wild capture fisheries, current understanding is dominated by predictions for individual species at coarse spatial scales. We show that species-specific responses to localized environmental changes will alter the collection of co-occurring species within established fishing footprints along the U.S. West Coast. We demonstrate that availability of the most economically valuable, primary target species is highly likely to decline coastwide in response to warming and reduced oxygen concentrations, while availability of the most abundant, secondary target species will potentially increase. A spatial reshuffling of primary and secondary target species suggests regionally heterogeneous opportunities for fishers to adapt by changing where or what they fish. Developing foresight into the collective responses of species at local scales will enable more effective and tangible adaptation pathways for fishing communities.

INTRODUCTION

Climate change is rapidly altering the structure and function of marine ecosystems (*1*, *2*). Ocean warming is occurring globally and is projected to continue throughout the 21st century (*3*). In concert, oceans are undergoing acidification and deoxygenation (*4*, *5*), as well as facing changes in timing and patterns of primary productivity and nutrient cycling (*6*). All of these physical and biogeochemical changes can alter the distributions and abundances of marine species (*7*) and can affect fisheries' productivity (*8*). Much progress has been made in projecting the effects of climate change, especially ocean warming, on marine species' distributions (*9*–*12*), and recent downscaled ocean climate models allow inference across multiple stressors at unprecedentedly fine scales [e.g., (*13*–*15*)]. By combining downscaled oceanographic models with species' environmental preferences, we can now elucidate important regional heterogeneity in projections of species distributions.

Understanding patterns of species redistribution with greater resolution, in turn, enables better projections of likely changes in the availability of economically valuable species to fisheries. However, the impacts of species redistribution on resource users can become complicated when considering multispecies harvest portfolios. Co-occurring species that are currently harvested as components of a multispecies complex may have similar or divergent responses to changing ocean conditions. Novelty in species responses can lead to complex reshuffling of species compositions across different fishing grounds, complicating management interventions. For example, if species that are already depleted from overfishing experience disproportionately large declines because of changing ocean conditions, then they could force management restrictions in unselective fisheries even when other species fare better [e.g., (*16*, *17*)]. Conversely, if low-value species are positively affected by climate change, then they could crowd fishing nets, making it harder for fishers to attain their allocated catches of higher-value, lower-abundance target species (*18*). Alternatively, if species within a complex have convergent (similar) responses to climate change, then this could weaken portfolio effects and impair the resilience of the multispecies complex to fishing pressure (*19*, *20*). Last, climate change could drive species into new areas where they are effectively unregulated and vulnerable to extensive harvest, which may reduce the species' ability to keep pace with the velocity of environmental change (*21*).

A spatial reshuffling of different harvested species will create diverse challenges for port-based fishers with limited mobility. Although fisheries are often assumed to "follow the fish", there are many practical, social, and regulatory constraints that can limit

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the mobility of fishers (*22*–*25*). For those fisheries that remain in historical fishing grounds, shifting fish distributions may reduce access to traditionally harvested species but increase access to others (*26*, *27*). Depending on the match or mismatch between fishing locations and species shifts, communities could experience a number of outcomes, including declines or gains in availability, or alterations in the composition of a multispecies complex. These outcomes may, in turn, require different adaptation measures by fishing communities and management agencies, such as changes in gear selectivity, changes in the location or timing of fishing activity, or switching to new target species. Adopting a multispecies lens to predict and manage changes in fisheries' availability can decrease long-term variance of catch and reduce risk of collapse at fishery or region-wide scales (*28*, *29*).

While the importance of understanding nuanced climate change effects on local availability of natural resources and the urgency of identifying implications of these changes for harvester adaptation are well established, few studies consider all of these factors simultaneously. Here, we investigate the multispecies groundfish fishery operating within the highly productive California Current ecosystem to understand how multiple climate-induced environmental changes will have complex cascading impacts from differential fish redistributions to fisheries' adaptations (*30*). We focus on four illustrative species within the multispecies U.S. West Coast groundfish fishery, comprising the Dover-thornyhead-sablefish (hereafter, DTS) complex. The complex includes sablefish *Anoplopoma fimbria*, the most valuable species, as well as Dover sole *Microstomus pacificus*, shortspine thornyhead *Sebastolobus alascanus*, and longspine thornyhead *Sebastolobus altivelis*. The four species are commonly harvested jointly on the outer continental shelf and slope and together account for 53% of bottom trawl groundfish revenue on the West Coast over the past 10 years (figs. S15 to S18). We used 8 years of fisheries' independent data from an annual trawl survey (*31*), combined with three downscaled Earth system models (ESMs) projected to 2100, to estimate how climate change will affect DTS species distributions and abundance in the future. Then, using records of spatial fishing locations for the U.S. West Coast bottom trawl fishery, we explored how regional heterogeneity and overlap between these fisheries' footprints and target species distributions may affect resource availability to the fishery and require adaptation by stakeholders in the future.

RESULTS

The California Current ecosystem is expected to experience significant warming ($\Delta T > 0$) and deoxygenation ($\Delta O < 0$) of bottom waters throughout the 21st century (Fig. 1A). Both temperature and oxygen have been shown to affect the occurrence and distribution of DTS species (*32*–*35*). To explore regional heterogeneity in expected climate change, we used three ESMs downscaled from the Intergovernmental Panel on Climate Change's Coupled Model Intercomparison Project Phase 5 (CMIP5) collection of models in a California Current implementation of the Regional Ocean Modeling System (CCROMS) (*15*). All three CCROMS-ESMs project warming within the California Current, with magnitudes of mean bottom temperature increases by 2100 ranging from <0.5°C under the Geophysical Fluid Dynamics Laboratory (GFDL) model to >1.1°C under the Hadley Center (HADL) model. For bottom oxygen, the projections are less consistent: While all models predict significant deoxygenation along the coastal margin of Washington and Oregon (where most commercial DTS landings occur), the HADL model diverges from the other two in its projection of a moderate increase in bottom oxygen in the central and southern portions of the California Current (fig. S15).

To assess how DTS species' abundance and distribution are likely to change under these projected changes in temperature and oxygen conditions, we fit ensemble species distribution models (SDMs) to historical bottom temperature and oxygen data and then projected them under the three CCROMS-ESMs. Each species' ensemble model constitutes a collection of four alternative SDMs with the same environmental predictors, but varied assumptions about the functional form of species-environment relationships and spatial covariates (see Materials and Methods for details). Instead of choosing a single best model for each species, we instead use a likelihood-based weighting scheme to combine the predictions from all models based on their relative out-of-sample predictive skill. Ensemble models offer the ability to explore model spread, thus quantifying the variability contributed by model parameterization (*36*).

Using these models, we find that the abundance trajectories for DTS species will likely diverge in the coming decades. Ensemble SDMs show with high confidence that expected environmental changes will cause sablefish and shortspine thornyhead to decline in abundance coastwide (i.e., throughout the entire study domain; Fig. 1A), while longspine thornyhead will increase in abundance (Fig. 1B). Dover sole is projected to increase in abundance under the GFDL and Institut Pierre-Simon Laplace (IPSL) models and decline slightly under the HADL model.

Projected coastwide shifts in abundance are important for assessing the general trajectory of a fish stock, but they can mask important local dynamics in stock distribution that are equally important to resource users and fisheries managers (*27*). Using SDMs to examine the spatial redistribution of DTS species, we find that all species except longspine thornyhead are projected to shift their distributions farther offshore into deeper areas; this pattern is particularly evident for areas north of ~45°N latitude (Fig. 2A and fig. S14). For shortspine thornyhead, the projected shift is as much as 20 km offshore at some latitudes. Offshore distributional shifts for DTS species are critically important from a fishery's perspective because of the relatively narrow shelf along the U.S. West Coast (*37*). Relatively small longitudinal shifts can be associated with substantial increases in depth for bottom-dwelling species. Fishing in deeper water strains the technical capacity of bottom trawl gear and makes fishing less efficient, and the greater distances traveled by vessels to fishing grounds becomes economically costly (*38*, *39*). Moreover, fishing deeper than the 700-fathom (~1280 m) isobath is currently prohibited under the groundfish fishery management plan (*40*). We project that the availability of sablefish and shortspine thornyhead shallower than 700 fathoms will decline substantially by 2100 (Fig. 2B and fig. S14). For sablefish in particular, already the DTS species with the deepest distribution, availability shoreward of the 700-fathom isobath will decline to <60% of its overall population by the end of the century under most simulations (down from approximately 70% from 1980 to 2010), while shortspine thornyhead will experience a similar, if less pronounced, shift to deeper water. Dover sole is likely to remain available at depths shallower than 700 fathoms, because its current distribution is shallower than the other DTS species.

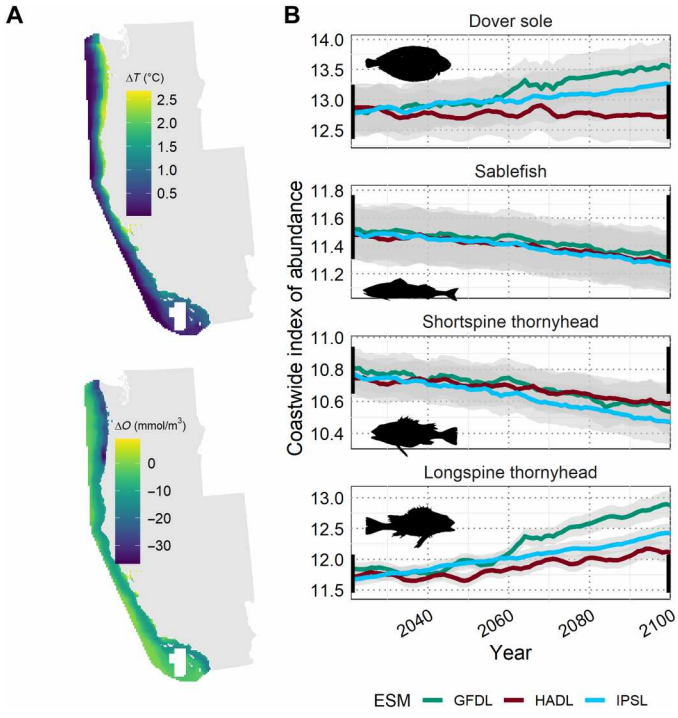

Fig. 1. Coastwide projections of bottom temperature, bottom oxygen, and species abundance. (**A**) Projected coast-wide change in bottom temperature (°C) and bottom oxygen (mmol/m^3), comparing the 2075–2100 mean to the 1985–2010 baseline period and presented as an ensemble mean across the three CCROMS-ESMs. (**B**) Projected ensemble abundance indices for the four DTS species under the three CCROMS-ESMs, presented as 5-year running averages. Solid lines are median projection values, and ribbons display ±1 SE. Black vertical bars denote the range of historical variability in the abundance index for each species from 1985 to 2010.

Although longspine thornyhead has a deeper distribution on average than all other DTS species except for sablefish, projected shifts in its depth distribution are more uncertain (Fig. 2B and fig. S14).

Coastwide, we have shown how changes in bottom temperature and oxygen are likely to drive shifts in the zonal, meridional, and depth distribution of multiple species. However, fishing occurs within distinct fishing grounds, and projecting changes in abundance on the grounds where trawl fishing actually occurs helps make potential climate change impacts more tractable for both fishers and managers. For all seven of the major U.S. West Coast fishing port groups examined (Fig. 3A and fig. S13), environmental conditions projected within their DTS fishing footprints by the end of the century are warmer and more hypoxic than the coastwide average (Fig. 3, B and C). The warming and deoxygenation of fishing grounds will create a mismatch between conditions within the fishing grounds and the empirical environmental niches (i.e., preferred conditions) of DTS species (Fig. 3C; see also figs. S2, S5, S8, and S11).

Not all species will shift to the same places and at the same rates: The relative availability to fisheries among DTS species will be reshuffled in space as species pursue the types of distributional shifts described above. Multiple shifting species distributions could create challenges for fisheries and managers because of the inherent nonselective nature of trawl fishing. In the U.S. West Coast groundfish trawl fishery, for example, sablefish and Dover sole are the common target species (fig. S19), with revenues far surpassing the revenue from the thornyhead species (figs. S15 to S17). However, these multispecies catches can come with bycatch trade-offs: Fishers targeting Dover sole can be constrained by sablefish in their nets, because regulations restrict the total allowable catch of sablefish in the trawl fishery (*41*). In addition, fisheries can encounter intraspecies bycatch problems when certain size classes are more valuable than others. Fishers targeting more valuable large sablefish sometimes encounter too many small, less-marketable sablefish, which can reduce overall revenue or incentivize the discarding of the smaller fish (*42*). From a fisher's perspective, these technical interactions, the bycatch of nontarget species and sizes, complicate the strategies and decisions vessels use to attain their quotas.

Species distribution shifts will alter opportunities for resource use (fishery targeting) in the future, and the effects will differ by port. For those fisheries that remain in historical fishing grounds, shifting fish distributions may reduce access to traditionally harvested species but increase access to others (*26*, *27*). For instance, we consider the projected changes in both availability (measured as density or catch per unit effort, CPUE) and multispecies overlap between Dover sole and sablefish in the two largest port-centric fishing footprints, for Astoria, OR and Fort Bragg, CA (Fig. 4). Because the environmental niche of Dover sole is much broader than that of sablefish (Fig. 3D) and because of geographic variability in projected environmental change (Figs. 1A and 3, B and C), we found that projected changes in Dover sole and sablefish abundance (Figs. 1B and 4A) and distribution (Fig. 2) will lead to reduced spatial overlap between the two species in Astoria and little change in Fort Bragg (Fig. 4B). Similar changes are projected within other West Coast fishing footprints (figs. S21 and S22). Although a reduction in overlap may imply that sablefish will be easier for fishers to target cleanly (i.e., with less risk of Dover sole bycatch), the overall projected reduction in sablefish biomass may offset any gains from the cleaner catch. Conversely, Dover sole may become easier to target within Astoria's fishing grounds as a result of increasing Dover sole abundance and decreasing overlap with sablefish. However, whether these changes will lead to a net benefit for Astoria's groundfish fishers will depend on market conditions for Dover sole, which is currently a marketable but low-value species (fig. S12).

DISCUSSION

Our accumulated evidence suggests that projected bottom temperature and oxygenation changes in the California Current (*15*) will lead to substantial shifts in the distributions and fisheries' availability of a key groundfish complex. A subset of key species will likely become more difficult to target for fishers as a result of a shift to deeper water, combined with a decrease in their abundance relative to lower-value species. Within U.S. West Coast fishing footprints, the availability of sablefish, the most valuable species in the DTS complex, is likely to decrease. Fishers operating out of each port will need to adapt their fishing behaviors, through changes in targeting or changes in fishing location (*43*), and will bear the associated costs of that adaptation. By quantifying the extent to which regional heterogeneity in climate impacts will influence the availability of fish to a multispecies fishery, we provide signposts for

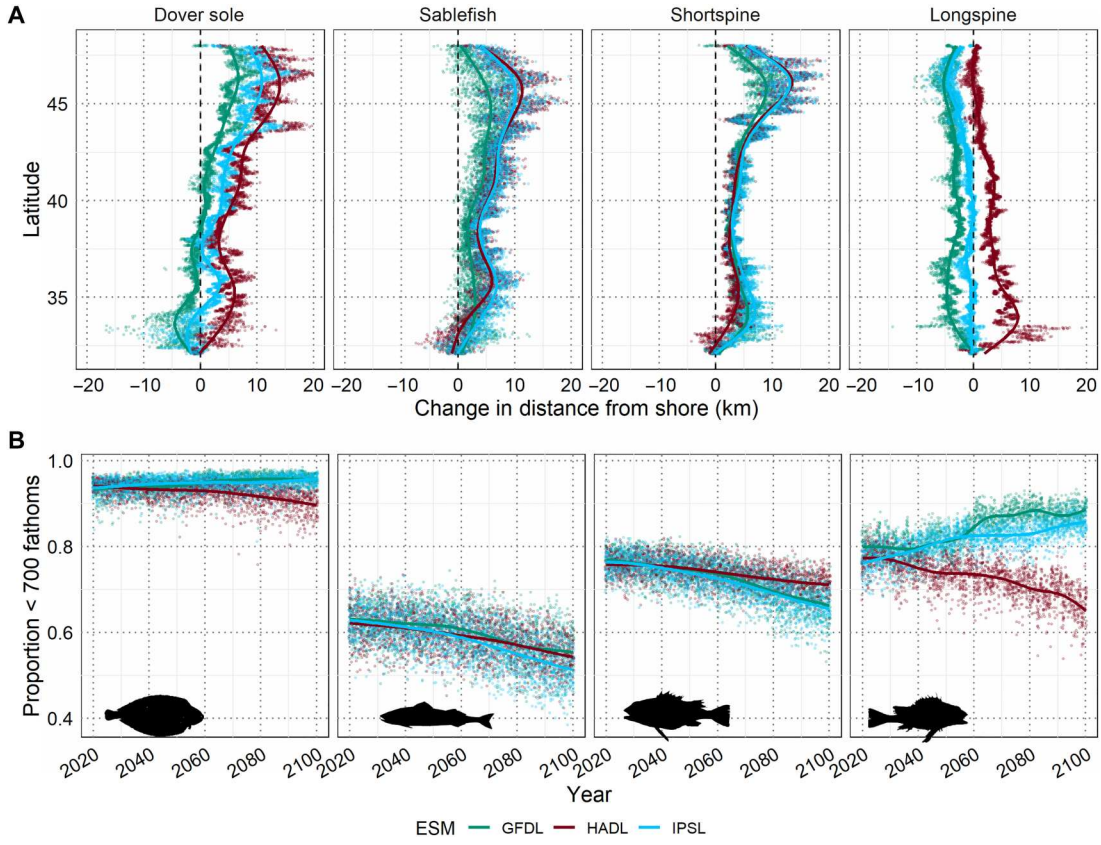

Fig. 2. Projected changes in DTS species' distance from shore and depth distributions. (**A**) Projected change in the weighted distance from shore centroid of species' distributions, comparing the 2075–2100 mean to the 1985–2010 baseline period. Values to the left and right of the dashed vertical line at 0 indicate species whose distributions are expected to shift onshore and offshore, respectively. Individual points indicate values from one simulation of the 100 performed for each species and CCROMS-ESM projection (panels). Lines are locally estimated scatterplot smooths. (**B**) Projected changes in depth distribution for each species, displayed as the proportion of summed catch in areas shallower than 700 fathoms, the current depth limit of allowable bottom trawling. Points and lines are as described in (A).

climate adaptation that would advance the goal of climate-ready fishery management.

Climate-driven species distribution shifts of the type presented here will require careful implementation of ecosystem-based fishery management measures (*44*). Approximately 90 groundfish species are currently managed by the Pacific Fisheries Management Council, across multiple commercial fishery sectors, each defined according to characteristics including access type (e.g., limited entry permit versus open access), target stocks, and gear type (midwater or bottom trawl, longline, pots, etc.). The Council uses a variety of management measures in the groundfish fishery, such as annual catch limits with subsequent allocation among distinct fishery sectors, individual fishery quotas, landings accumulation limits, season lengths, potential spatial closures, and gear restrictions among others (*45*–*49*). Many of these management measures may need to be evaluated to assess their efficacy under climate change and to identify ways to maximize flexibility for fishers to adapt while safeguarding climate-vulnerable fish stocks.

Spatial management measures such as temporary or permanently closed areas are one avenue for adaptive management. The efficacy of spatial closures is difficult to evaluate (*50*, *51*), but our results suggest that existing management measures should be reevaluated over time. For example, areas closed within specific depth zones are likely to vary in effectiveness as species shift and will need to be reassessed to ensure that they are continuing to support sustainable fishing opportunities as some important species shift deeper. In 2002, a series of depth-based closed areas known as Rockfish Conservation Areas (RCAs) was instituted across the U.S. West Coast to protect vulnerable rockfish species from overexploitation. In 2020, many of these areas were reopened as a result of the successful rebuilding of many rockfish stocks, combined with a shift toward quota-based management. Theoretically, the opening of these areas for trawl fishing will allow fishers more flexibility in the depths and the species they can target in coming years and decades. However, with the intensifying stressor of climate change, it is also possible that closures similar to the RCAs could represent important spatial refugia for shifting species. It is tradeoffs similar to these between conservation and fisher flexibility that form the basis of climate-ready considerations for managers. Likewise, the largest spatial closure to groundfish fishing is the restriction of fishing at depths greater than 700 fathoms (*40*). Fishing at such depths is technically challenging (*38*) and currently illegal, but if a large proportion of target species' biomass moves deeper, as our results suggest for some species, there may be an incentive for industry and management to address technical, legal, and policy challenges to enable fishing at greater depths.

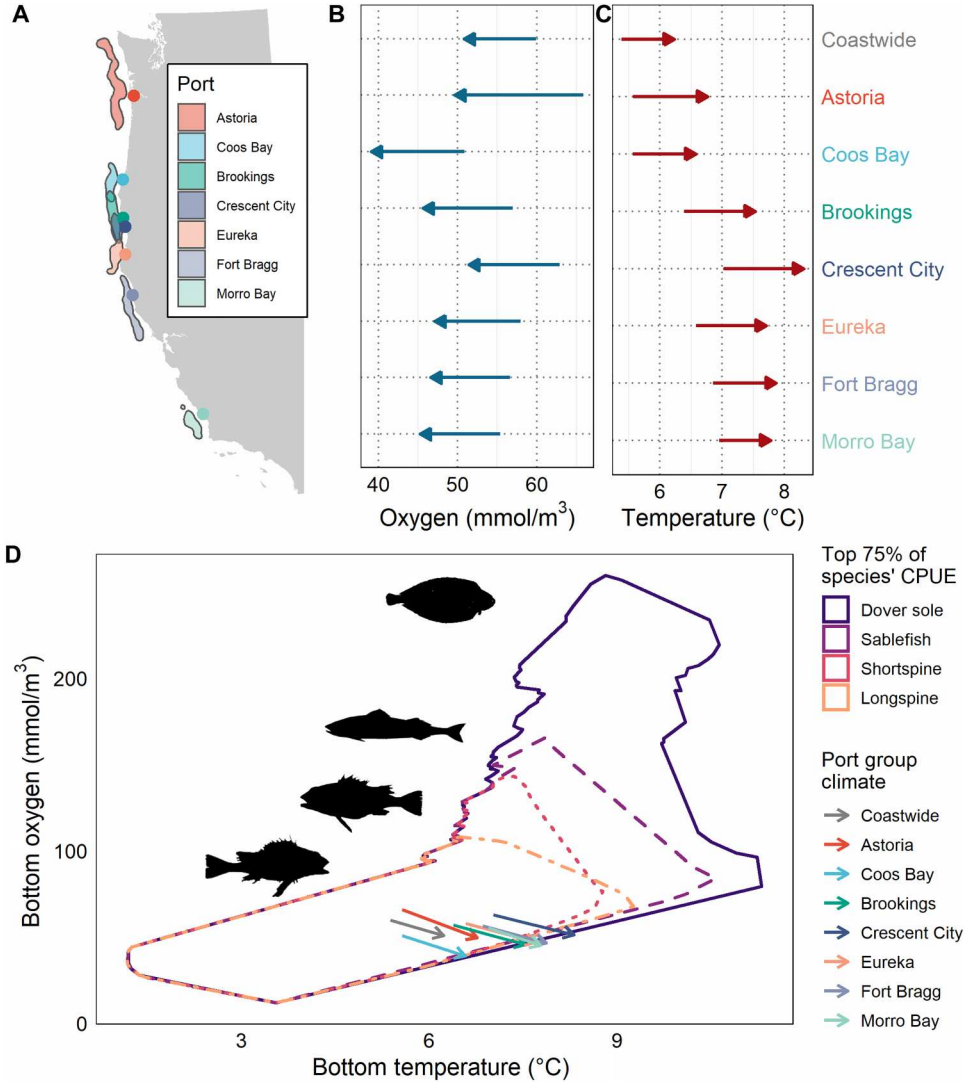

Fig. 3. Projected environmental change within fishing footprints. (**A**) Trawl fishing footprints of major U.S. West Coast ports targeting DTS species. Projected change in (**B**) mean bottom oxygen (mmol/m^3) and (**C**) mean bottom temperature (°C) coastwide and within specific fishing footprints, based on an ensemble mean across the three CCROMS-ESMs. Arrows represent change from a 1985–2010 mean to a 2075–2100 mean. (**D**) Empirical environmental niches of DTS species. Outlines encompass the 75th percentile of each species' estimated biomass density values from 1985 to 2010 in environmental state space. Arrows indicate the same climate changes as (B) and (C) within fishing footprints.

Fishers who cannot or decide not to shift their fishing footprints in lockstep with their target species could alternatively alter their target catch (*43*). Sablefish and Dover sole are important target species in the groundfish fishery (fig. S19), but fishing portfolios and strategies could certainly change in the future. These changes are already occurring in many regions, exemplified by the emergence of new fisheries in the United Kingdom and on the U.S. East Coast in recent years in response to climate change (*52*, *53*). Shifts in fishers' target species are happening on the U.S. West Coast as well, where recent warming and marine heat waves have led to a rapid expansion of the range of market squid *Doryteuthis opalescens* and its associated fishery (*54*). Many fishers that participate in the DTS fishery have diverse harvest portfolios, operating in fisheries for crab, shrimp, and other groundfish species across different seasons of the year (*55*, *56*). This diversification provides fishing communities with revenue throughout the year, but fishing portfolio diversification comes with its own set of challenges. Switching fishing gear to target new species or sizes is difficult and expensive. Recent analyses for West Coast fishers suggest that it is temporal diversification, the ability to fish across an array of fisheries during different times of year, which primarily buffers against income variability, meaning that disruptions to a single fishery could affect this intra-annual stability and the longer-term resilience it may support (*57*). Moreover, the rapid pace of some climate-driven distribution shifts may challenge the ability of the fishers, the seafood processing industry, and the fishery management system to adapt (*43*, *58*, *59*). Nevertheless, depending on the velocity of distributional shifts and fishery adaptive capacity, we may see a shift toward portfolios targeting species with warmer

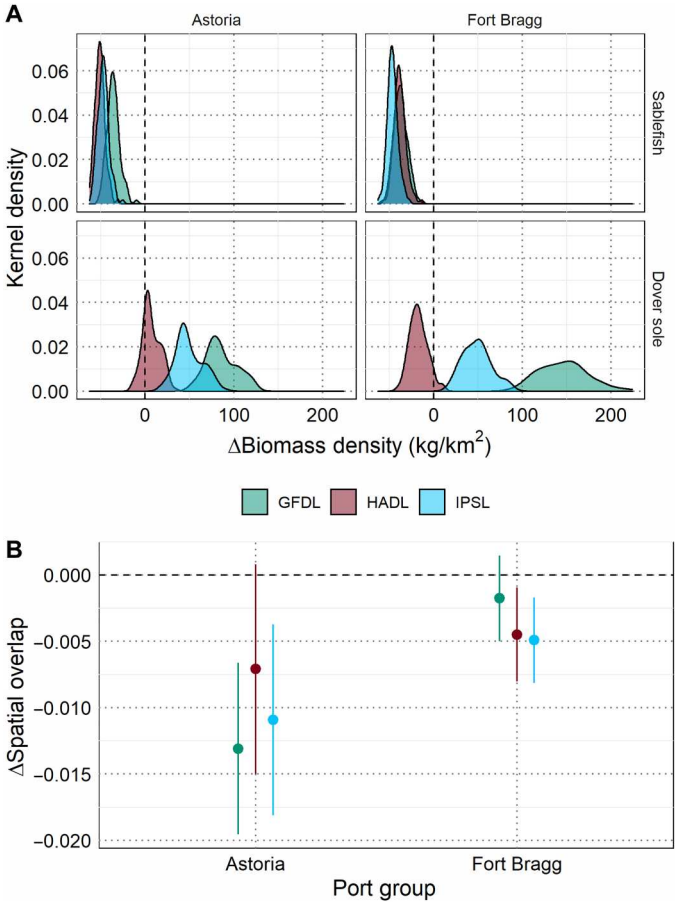

Fig. 4. Changes in Dover sole and sablefish biomass density and overlap. (**A**) Projected percent change in density from a 1985–2010 mean to a 2075–2100 mean for sablefish and Dover sole in the Astoria and Fort Bragg fishing areas, under alternative CCROMS-ESMs projections. (**B**) Change in spatial overlap between sablefish and Dover sole within the same footprints and time periods, measured by the Bhattacharyya's coefficient. Points below the dashed line at zero represent reduced overlap in future projections compared to the historical mean. Error bars represent the distribution of change in overlap across the 100 draws from the joint parameter distribution for each species and CCROMS-ESM projection.

temperature and lower oxygen tolerances and a corresponding decrease in targeting of some valuable species such as sablefish.

Regardless of the particular strategies chosen, fisheries and management adaptation may be most successful if tailored to be region specific. In regions where valuable target species move further offshore, additional development of deeper fishing techniques may be required, or else fishers could switch to more accessible species. In other places with changing availability but a more consistent overlap between species, the desired adaptation may focus more on technical solutions (e.g., gear modifications) to increase fishery selectivity. Last, shifting fisheries will inevitably come into conflict with other emerging ocean uses. Offshore wind and wave renewable energy and offshore aquaculture are developing rapidly (*31*, *60*, *61*) and will undoubtedly create areas of the ocean where groundfish fishing will not be possible, particularly for trawl fisheries. Our results suggest that projections of species' future distributions will be important in the decision-making process for where these new sectors are permitted and sited to minimize future conflict across ocean use sectors and the conservation and management of fisheries' species.

Ensemble SDMs and multiple climate change projections helped to bound important elements of uncertainty in our study. Within our SDM ensembles, differences across the three climate models contributed more uncertainty in our results than did uncertainty in our fitted model parameters (e.g., Fig. 1B), but this may not always be the case for all species or in other geographies (*36*). The variation in our projections represents a range of plausible futures, and we would therefore recommend the multimodel or ensemble approach to other SDM practitioners. Future studies using SDMs should continue to assess multiple model types or formulations and consider alternative climate models or at least present their results with appropriate caveats (*62*, *63*). Furthermore, climate change will affect other key aspects of fish stock productivity that are beyond the scope of this study, including alterations to age and size structure, ontogeny, recruitment, and food web structure [e.g., (*64*–*66*)]. Climate-ready management will benefit from scientific advice that addresses this suite of changes (*28*).

Climate change is increasingly requiring fisheries to reckon with new biological and ecological realities. Using robust, data-driven models to inform our expectations of future changes in key species distributions, as well as assessing how those changes may manifest within established fishing footprints, provide a proactive approach toward climate-resilient ocean management. More broadly, development of approaches that allow insight into the collective responses of species to climate change in localized areas creates opportunities for developing more tangible, proactive, and effective adaptation strategies. Ensemble SDMs combined with multiple climate projections and community-specific information about resource reliance can help set expectations, appropriately bounded by uncertainty, for important harvested species and human activities in the future.

MATERIALS AND METHODS

Overview

The goal of our analysis was to combine trawl survey and fishery-dependent landings data with hindcast and projected environmental data, through state-of-the-art SDMs, to understand the current and future distributions of key groundfish species caught in the U.S. West Coast bottom trawl fishery. Our workflow, described in detail below, was to (i) fit four geostatistical models with environmental variables as predictors to explain the spatiotemporal variability in CPUE for each species of interest, (ii) generate realizations of future environmental conditions in the California Current using three ESMs, and (iii) combine future models of the environment with current models of fish distribution to project species distribution responses to climate change. We used these model projections to estimate (i) abundance across time to 2100 under diverging climate projections, (ii) changes in spatial distribution of species in three dimensions (latitude, longitude, and depth), (iii) changes in environmental conditions within current-day fishing footprints and their relationship to species' modeled environmental affinities, and lastly, (iv) changes in the relative overlap among species' distributions over time. In the following, we describe the details of how the data were analyzed and how the species models were fitted, with associated measures of uncertainty.

Study region and species

We studied groundfish species distributions within the U.S. waters of the California Current. The California Current Large Marine Ecosystem spans 3000 km of coastline (*67*) within which commercially valuable marine species are found off the coasts of the U.S. states of Washington, Oregon, and California. Commercial fisheries in these areas generated $635.6 million in 2018. The diverse group of species in the Pacific Coast Groundfish Management Plan (*40*) has been important foci for commercial fishing activities for numerous West Coast ports (*55*). Within the groundfish trawl fishery, we focus on the species complex of Dover sole *M. pacificus,* shortspine thornyhead *S. alascanus,* longspine thornyhead *S. altivelis*, and sablefish *A. fimbria*, species that together comprise the DTS complex. The DTS complex is a common target of the U.S. West Coast groundfish fishing (fig. S19), with sablefish representing a relatively low-volume but high-value target and Dover sole representing a low-value but high-volume target.

Data sources

Species landings and value

Fisheries' landings data for the focal study species were downloaded from the NOAA Fisheries online data portal (www.fisheries.noaa.gov/national/sustainable-fisheries/commercial-fisheries-landings). These data include landings by U.S. state, year, and species. We combined the landings from all ports in each of the three U.S. West Coast states (California, Oregon, and Washington) to obtain overall landings value for each year from 1980 to 2020 for DTS species.

Trawl survey data

Data on species occurrence and density used in SDMs come from the West Coast Bottom Trawl Survey (WCBTS) long-term, standardized trawl survey conducted by the National Oceanic and Atmospheric Administration (NOAA)'s Northwest Fisheries Science Center (*68*). Although other trawl surveys have existed in some form since the late 1970s, the WCBTS has used consistent sampling gear, spatial sampling protocols, and methods annually since 2003 to assess species' abundances, size structure, and age composition with a random stratified design. The SDMs described below used observed CPUE (in kg/km^2) from the trawl survey for the four species comprising the DTS complex, where effort is defined as area swept by the survey gear. The term CPUE in our study is therefore interchangeable with modeled biomass density.

Downscaled climate projections

Environmental predictors for SDMs were extracted from a California Current configuration of the Regional Ocean Modeling System (hereafter referred to as CCROMS) (*69*, *70*) coupled with a biogeochemical model (NEMUCSC, a University of Santa Cruz model based on the North Pacific Ecosystem Model for Understanding Regional Oceanography, NEMURO) (*71*, *72*), which is a customized version of the North Pacific Ecosystem Model for Understanding Regional Oceanography (*73*). The CCROMS domain covers 30° to 48°N inshore of 134°W, with a 0.1° (7 to 11 km) horizontal resolution and 42 terrain-following vertical depth levels (*15*, *74*). In this study, we used four different numerical simulations of the CCROMS: a hindcast for 1980–2010, which provides realistic historical ocean conditions used for model fitting, and three downscaled climate projections for 1980–2100, which provide future ocean conditions to infer species distribution changes with SDMs.

To create the climate projections, CCROMS was forced by output from three ESMs selected from the CMIP5. Specifically, we use output from the IPSL CM5A-MR, HADL HadGEM2-ES, and GFDL ESM2M ESMs under the high-emissions Representative Concentration Pathway 8.5 (RCP8.5) scenario (*75*). These models were selected to represent the spread of physical and biogeochemical futures in the CMIP5 ensemble. The GFDL and HADL models represent opposite ends of the spectrum for the projected magnitude of warming in the CMIP5 ensemble (*15*, *76*). The warming in GFDL under RCP8.5 is similar to the CMIP5 ensemble mean temperature increase under the RCP4.5 scenario. Moreover, for biogeochemical variables, the range of projections under the RCP2.6 and RCP4.5 scenarios is largely contained within the model uncertainty under the RCP8.5 scenario. Further details on the downscaled hindcasts and projections are found in (*15*).

We extracted bottom temperature and bottom oxygen from the CCROMS hindcast to match trawl survey times and depths. CCROMS values of temperature and oxygen were smoothed with a 30-day running mean to reduce the variance associated with extractions from individual model days. Because the CCROMS model does not perfectly capture underlying bathymetry (because of its 0.1° resolution), we first ensured that we were extracting environmental data from appropriate depths. Specifically, for each observation (i.e., a single tow of the survey trawl), we first found the CCROMS cell closest to the location and time of the trawl. If the observed trawl depth was shallower than the "bottom" (deepest depth layer) of the CCROMS model, then we extracted linearly interpolated temperature and oxygen values corresponding to the trawl depth. If the observed trawl depth was deeper than the bottom of the CCROMS, then we moved to the nearest model grid cell with bottom depth equal to or greater than the trawl depth and performed the extraction there. In simple terms, we extracted values from CCROMS that most closely matched observed trawl locations and times, while ensuring that we extracted values from appropriate depths.

Species distribution models

We used the R package sdmTMB (*77*) to construct SDMs and make ensemble predictions of future spatial distributions for the species in the DTS complex. The sdmTMB package implements the Stochastic Partial Differential Equation approach (*78*) to approximating spatial Gaussian random fields as developed in the Integrated Nested Laplace Approximation R package (*79*). sdmTMB fits the models with maximum marginal likelihood through the Template Model Builder (*80*). We constrained the spatial domain for both SDM fitting and projection to the overlap between the CCROMS model domain and the trawl survey extent (Fig. 1). We fit SDMs to WCBTS data for the years 2003–2010, which spans the overlapping period between the beginning of current methods in the trawl survey (2003 to present) (*68*) and the end of the CCROMS hindcast (1980–2010) (*15*).

We fit four alternative SDMs to WCBTS data from each species. For each candidate model, we used the same environmental predictors but varied assumptions about the functional form of species-environmental relationships and spatial covariates. The general form of the SDMs is a generalized linear mixed model (GLMM)

and can be written as

$$E[y_s] = \mu_s$$

$$\mu_s = g^{-1}(\mathbf{b}_s{}^T \mathbf{X}_s + \omega_s) \quad (1)$$

where y_s represents a CPUE observation at location s, μ_s represents the expected value, $g^{-1}()$ represents an inverse link function, $\mathbf{b}_s$ represents a vector of estimated coefficients, $\mathbf{X}_s$ represents a vector of associated covariates, and ω_s represents an optional spatial field. Because trawl survey data are often zero-inflated with skewed catch rates, previous research has either fit delta-GLMMs or used a Tweedie distribution to model combined zeros and positive catches (*81*). We adopted the Tweedie distribution here because it involves estimation of a single latent spatial field. Our four alternative model configurations included models with and without an estimated spatial field (ω_s) and covariates (oxygen and temperature) modeled either as a quadratic function or as a smooth function. Ideally, environmental covariates would explain nearly all variation in the data; however, as some biological processes may not be perfectly represented with oxygen and temperature, the latent spatial field represents additional variation in density not explained by these covariates. Penalized splines (*82*) were used to model the covariates as an alternative to the quadratic; low-dimensional versions of these models (e.g., $k = 3$) result in similar functional relationships to the quadratic (*83*). Additional model complexity, such as spatiotemporal variation, or temporal covariates (e.g., year fixed effects or autoregressive terms) were not used in fitting because of difficulties in projecting these effects many years in the future.

We visualized and quantified model fit using percent deviance explained, using relative log-likelihood between models, and by visually inspecting randomized quantile residual plots (figs. S1, S4, S7, and S10) (*84*). Although the models varied in their percent deviance explained relative to an intercept-only null model, note that higher deviance explained for historical data does not always indicate strong predictive performance for SDM projection models under climate change (*54*, *85*). We instead quantified the predictive ability of each model for each species by splitting data into a test and training set and using the test set to compute the predictive density. Test and training partitions were generated by assigning 10% of observations randomly to the test set, ignoring effects of space and time (but using the same splits for a given species across models). After fitting the model to the training data, the total predictive density for each model m was calculated as the product of likelihoods for the test set

$$\lambda_m = \prod_{i=1}^{n} L(y_i | \theta) \quad (2)$$

where $L()$ corresponds to the Tweedie likelihood and θ represents estimated parameters. Predictive densities across models were then used to generate ensemble predictions, using a likelihood-based stacking approach from the Bayesian literature, described in (*86*). This approach maximizes the quantity

$$\sum_{i=1}^{m} p_m \lambda_m \quad (3)$$

where the vector p represents estimated compositional weights for each model. These model weights were used to produce spatial residual maps to assist in model validation (figs. S3, S6, S9, and S12). Within each species' ensemble, we extracted residuals from each individual model fit and then combined them using the likelihood-based weights to produce a single map. The spatial residual maps generally showed no evidence of consistent spatial bias. The one exception was the map for longspine thornyhead (fig. S12), which shows some evidence of consistent underprediction in offshore areas of the central California Current.

We made ensemble CPUE predictions using the model weights from Eq. 3 (tables S1 to S4), projected onto annual bottom temperature and bottom oxygen fields extracted from the IPSL, GFDL, and HADL CCROMS model projections (years 1980–2100) (*15*). In the projections, environmental data included July mean bottom temperature and oxygen from the CCROMS model for each prediction location, representing approximately the midpoint of the trawl survey season. Using these July means, we made one ensemble prediction for each species per location per year, meaning that, in practice, we made species distribution predictions for each boreal summer. The final prediction grid has 2212 spatial cells for each projected year. This approach to predict CPUE onto a grid is identical to the index standardization process commonly used in fisheries' assessments to estimate historical changes in biomass.

We quantified uncertainty because of both the SDM model fits and the potentially diverging ESMs. To approximate parameter uncertainty, we took 100 draws from each model's joint precision matrix and applied the ensemble weighting (Eq. 3) to each draw. Then, to compare the impact of parameter uncertainty and diverging ESMs, we projected each ensemble draw through the GFDL, HADL, and IPSL ESMs.

Species-environment relationships and distribution shifts

To calculate each species' estimated environmental niches with respect to bottom temperature and oxygen, we used the ensemble CPUE predictions described above. We compared species-environment relationships by calculating and visualizing the range of bottom temperature and oxygen values that encompass the top 75% of each species' estimated CPUE during the 1985–2010 historical period, using concave hulls as implemented in the concaveman package in R (*87*). Similar plots for other percentage cutoff values for each DTS species are provided in the Supplementary Materials.

Using SDM outputs and their relative model weights, we tracked shifts in species distributions in three dimensions (latitude, longitude, and bottom depth) through projected time. We calculated each species' depth distribution and the zonal (latitudinal) distance from the coast of the species' distribution centroid. For the distance from the coast calculation, the centroid within a given latitude band was calculated as the mean distance from shore of the CCROMS cells in that band, weighted by predicted species' CPUE.

Fishing footprint analysis

Fishing port–specific fishing footprints were defined as the area fished for all trips that landed their catch within a specific group of fishing ports. Port groups were adopted from a classification commonly used by U.S. West Coast fisheries managers, defined in specifications for the Input-Output Model for Pacific Coast Fisheries (*88*). All fishing trips associated with the port group that caught Dover sole, thornyhead, and sablefish were extracted from the Pacific Fisheries Information Network (https://pacfin.psmfc.

org/) logbook data. While logbook reporting has less than a 100% compliance rate, we assume that the available data accurately captures the relative spatial distribution of fishing effort. Focal port groups—Astoria, Coos Bay, Brookings, Crescent City, Eureka, Fort Bragg, and Morro Bay—were selected on the basis of the high volume and relative importance of DTS to total landings in these ports (figs. S13 and S19). To determine spatial fishing footprints, total quantity landed was aggregated across DTS species for each fishing trip. The latitude and longitude coordinates for each catch location were converted to a Universal Transverse Mercator zone 10 projection to allow for more accurate estimates of distance, area, and spatial overlap. A weighted, two-dimensional kernel density surface was created from the point estimates of catch for the period 2011–2019 with a 10 km bandwidth, using the density.ppp function in the sp package in R (*89*). The 2011–2019 time period was chosen for defining the fishing footprints because of a major regulatory change that instituted catch share management in the U.S. West Coast groundfish fishery (*90*). The footprint of each port group was defined using a percent volume contour representing the boundary of the area that contains 75% of the volume of the kernel density distribution using the getvolumeUD function in the adehabitat package in R (*91*).

We calculated changes under both projected environmental conditions and species distributions within these port-specific fishing footprints. Change in species′ availability was measured as the percent change in mean CPUE between a 1985–2010 baseline mean and a 2075–2100 future mean. We calculated these changes for each of the four DTS species. We also calculated the change in overlap between pairs of species within each fishing footprint between the same time periods to measure deviations in projected species co-occurrence. To measure overlap, we used Bhattacharyya′s coefficient (*92*). Bhattacharyya′s coefficient is defined as

$$\sum_{i}^{n} \sqrt{p_{1,i} p_{2,i}} \tag{4}$$

where $p_{1,i}$ is the proportion of the total biomass of species 1 in grid cell i. The metric measures the extent of statistical affinity between two distributions and can be interpreted as assessing whether the two species use space independently of one another (*92*). For each fishing footprint in each year, we calculated the value of Bhattacharyya′s coefficient for each pair of species across all i grid cells in each footprint. Then, following our convention in the other calculations described above, we assessed the change in overlap between a 1985–2010 baseline mean and a 2075–2100 future mean.

Supplementary Materials

This PDF file includes:

Supplementary Text
Figs. S1 to S22
Tables S1 to S4

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