ICES Journal of Marine Science

ICES Journal of Marine Science (2020), 77(6), 2118–2133. doi:10.1093/icesjms/fsaa103

Original Article

Characterizing uncertainty in climate impact projections: a case study with seven marine species on the North American continental shelf

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Morley, J. W., Frölicher, T. L., and Pinsky, M. L. Characterizing uncertainty in climate impact projections: a case study with seven marine species on the North American continental shelf. – ICES Journal of Marine Science, 77: 2118–2133.

Received 15 November 2019; revised 20 May 2020; accepted 25 May 2020; advance access publication 8 August 2020.

Projections of climate change impacts on living resources are being conducted frequently, and the goal is often to inform policy. Species projections will be more useful if uncertainty is effectively quantified. However, few studies have comprehensively characterized the projection uncertainty arising from greenhouse gas scenarios, Earth system models (ESMs), and both structural and parameter uncertainty in species distribution modelling. Here, we conducted 8964 unique 21st century projections for shifts in suitable habitat for seven economically important marine species including American lobster, Pacific halibut, Pacific ocean perch, and summer flounder. For all species, both the ESM used to simulate future temperatures and the niche modelling approach used to represent species distributions were important sources of uncertainty, while variation associated with parameter values in niche models was minor. Greenhouse gas emissions scenario contributed to uncertainty for projections at the century scale. The characteristics of projection uncertainty differed among species and also varied spatially, which underscores the need for improved multi-model approaches with a suite of ESMs and niche models forming the basis for uncertainty around projected impacts. Ensemble projections show the potential for major shifts in future distributions. Therefore, rigorous future projections are important for informing climate adaptation efforts.

Keywords: black sea bass, climate change, market squid, sablefish, species distribution modelling

Introduction

Earth system model (ESM) simulations are frequently used to forecast climate change impacts on natural resources (Stock *et al.*, 2011; Pacifici *et al.*, 2015). Projecting climate impacts on species generally requires the coupling of species distribution models with ESM simulations of future environmental conditions. Such studies are computationally complex and expensive, and they often simulate climate impacts on hundreds of species simultaneously (Thuiller, 2004; Cheung *et al.*, 2009; Diniz-Filho *et al.*, 2009; Morley *et al.*, 2018; Thuiller *et al.*, 2019). The interpretation of projected climate impacts on natural resources, and in particular, the incorporation of such information into policy decisions is still in its infancy (Guisan *et al.*, 2013; Bonebrake *et al.*, 2018; Miller *et al.*, 2018). However, it is clear that the effective quantification of uncertainty inprojected climate impacts is critical for the assessment of suchforecasts by end users (Thuiller, 2004; Araujo and New, 2007; Buisson *et al.*, 2010; Cheung*et al.*, 2016a; Thuiller *et al.*, 2019).

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Despite broad recognition that quantifying uncertainty in species projections is important, relatively few studies have comprehensively characterized uncertainty (but see, Dormann *et al.*, 2008; Buisson *et al.*, 2010; Thuiller *et al.*, 2019). Projection uncertainty comes from multiple sources and—depending on the spatial and temporal scope of the study and the biological data used—any one of them may be important (Hawkins and Sutton, 2009; Cheung *et al.*, 2016a). For instance, several options are available for future scenarios of socio-economic developments and associated greenhouse gas emissions (Riahi *et al.*, 2017). Also, a suite of different ESMs is available that each simulates future climates based on inputs from future greenhouse gas emission scenarios. The structure of ESMs varies in many ways, including spatial and temporal resolution, and how fine scale oceanographic features like oceanic currents are parameterized (Stock *et al.*, 2011). Finally, structural uncertainty from biological models can impact projections because there are often multiple options available for representing species habitat associations or population dynamics (Thuiller, 2004; Diniz-Filho *et al.*, 2009; Buisson *et al.*, 2010; McHenry *et al.* 2019; Brodie *et al.* 2020). Furthermore, parameter uncertainty within biological models may represent an important source of variation (Hare *et al.*, 2012b). Another important consideration is that the characteristics of uncertainty may vary spatially, such that confidence in a species' projection may be high in one geographic area and poor in another (Diniz-Filho *et al.*, 2009; Buisson *et al.*, 2010; Raybaud *et al.*, 2017).

Collectively, climate projection studies show the potential for major impacts on living resources and regional or global threats to biodiversity during the 21st century (Pereira *et al.*, 2010; Pörtner *et al.*, 2014; Jones and Cheung, 2015; García Molinos *et al.*, 2016; Lotze *et al.*, 2019). Management structures that are designed to promote the sustainable use of natural resources will be challenged. For example, the effectiveness of conservation areas may be compromised with the redistribution of habitats (Araujo *et al.*, 2011), and there will be significant challenges faced by all sectors of the fishing industry as species shift and regional productivity changes (Cheung *et al.*, 2010, 2016b; Pinsky *et al.*, 2018; Lotze *et al.*, 2019). Therefore, there is a critical need for studies that conduct detailed characterizations of projection uncertainty to inform the implementation of climate-adaptive resource management (Araujo and New, 2007; Cheung *et al.*, 2016a; Thuiller *et al.*, 2019).

We conducted a comprehensive analysis of projection uncertainty with seven economically important species. Specifically, we simultaneously investigated the relative importance of four sources of uncertainty, including future greenhouse gas emissions scenario, ESM model structure, niche modelling approach, and parameter uncertainty in the species environmental relationships. For each species, we conducted 8964 high-resolution (~30 km^2) projections of suitable habitat shifts during the 21st century over a geographically broad spatial grid that encompassed over 1.1 million km^2 for Pacific coast species and over 1.8 million km^2 for Atlantic coast species (including the Gulf of Mexico). We show that the most important sources of uncertainty vary among species, future time periods, geographic regions within a species' range, and metrics used to quantify projected changes.

Methods

The projections for shifts in habitat conducted here are based on the framework that was developed in Morley *et al.* (2018), where projections for >680 marine species on the North American continental shelf are examined. Therefore, we provide a briefer description of aspects of the methodology that were similar to Morley *et al.* (2018). Here, we used the same biological dataset for species distribution modelling. The climate projection data that we used represent an expanded set of future simulations compared to our previous study.

Modelled species

We conducted our analysis with seven species, although the results from three of these are primarily in the Supplementary Material. From the Pacific we analysed Pacific halibut (*Hippoglossus stenolepis*), Pacific ocean perch (*Sebastes alutus*), sablefish (*Anoplopoma fimbria*), and California market squid (*Doryteuthis opalescens*). From the Atlantic we analysed summer flounder (*Paralichthys dentatus*), American lobster (*Homarus americanus*), and black sea bass (*Centropristis striata*). All of these species are of substantial economic importance. For instance, American lobster is presently the most valuable species to US commercial fisheries, while Pacific halibut and sablefish are two of the most valuable finfish (National Marine Fisheries Service, 2018). Furthermore, summer flounder and black sea bass are valuable recreational fisheries. We chose Pacific ocean perch to represent a species from the diverse *Sebastes* complex, and California market squid were chosen because it is the most valuable US squid fishery. These seven species also represent a range of thermal niches on each coast and a range in the number of survey observations available (Table 1 and Supplementary Table S1).

Survey and environmental data

Species occurrence and biomass data were taken from a curated dataset of 135 254 bottom trawl hauls from 20 long-term surveys that encompassed most of the continental shelf area of the United States and Canada (Morley *et al.*, 2018). Each trawl haul was coupled with a suite of environmental data based on the date and geographic location of each sample. Sea surface temperature (SST) and sea bottom temperature (SBT) variables were obtained from the Simple Ocean Data Assimilation (SODA3.3.1 for 1980–2015 and SODA2.2.4 for pre-1980) reanalysis of ocean climate, which provides a global reconstruction of past ocean temperatures (Carton *et al.*, 2018). Two variables were used to describe seafloor characteristics at the location of each trawl. Rugosity, which measured spatial variation in depth at a ~5.6 km spatial scale, was calculated using depth data from the GEBCO gridded bathymetric data set (Becker *et al.*, 2009). Sediment grain size was used to describe benthic habitat and consisted of either geographic point values or polygon-based maps (Morley *et al.*, 2018). Point values were interpolated using inverse distance weighting to obtain sediment data that matched the resolution of the rugosity data.

Species niche modelling

To model species' realized niches, we used three approaches with R software version 3.5.0 (R Core Team, 2018). First, generalized linear models (GLMs) were used in which all continuous predictor variables were modelled with both linear and quadratic terms.

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Table 1. Evaluation of six niche models for four species, including the proportion of deviance explained for a probability of occurrence and a biomass model for each of three statistical approaches: GLM, GAM, and BRT.

	Deviance explained		Test data metrics			R^2 survey-year means	
Model	**Prob. Occ.**	**Biomass**	**AUC**	**$TSS_{(max)}$**	**$kappa_{(max)}$**	**Prob. Occ.**	**Delta-biomass**
Pacific halibut ($N = 19\,437$ observations; $N = 0$ near-zero values added)							
GLM	0.32	0.28	0.86	0.57	0.57	0.84	0.71
GAM	0.33	0.28	0.87	0.59	0.59	0.87	0.72
BRT	0.39	0.34	0.89	0.63	0.63	0.88	0.75
Pacific ocean perch ($N = 8\,340$ observations; $N = 0$ near-zero values added)							
GLM	0.36	0.21	0.89	0.65	0.60	0.89	0.97
GAM	0.38	0.22	0.89	0.64	0.58	0.89	0.98
BRT	0.47	0.34	0.92	0.68	0.62	0.94	0.91
Summer flounder ($N = 12\,200$ observations; $N = 2\,954$ near-zero values added)							
GLM	0.47	0.74	0.93	0.76	0.59	0.86	0.01
GAM	0.46	0.86	0.94	0.79	0.60	0.83	0.00
BRT	0.54	0.97	0.95	0.82	0.64	0.82	0.73
American lobster ($N = 11\,994$ observations; $N = 3\,157$ near-zero values added)							
GLM	0.27	0.76	0.89	0.68	0.45	0.75	0.80
GAM	0.31	0.85	0.90	0.67	0.47	0.75	0.28
BRT	0.42	0.94	0.93	0.73	0.57	0.80	0.85

Also shown are evaluation metrics where niche models were applied to independent test data, which includes R^2 values for relating predicted vs. observed survey-year mean values.

GLMs represent a relatively simple modelling approach with a low risk of overfitting. Furthermore, the GLMs assume that species relationships with environmental variables are relatively simple (e.g. dome shaped). Second, generalized additive models (GAMs) were fit with the *mgcv* R-package (Wood, 2011), which represent an approach of intermediate complexity. More complex relationships with predictors can be achieved with GAMs, although there is greater risk of overfitting than with GLMs. To reduce overfitting, we applied a gamma penalty against model complexity that was equal to the log of the number of samples divided by 2. Also, a shrinkage penalty was used that acts on individual model terms such that they can be removed from the model.

The third niche modelling approach was boosted regression trees (BRT) with the *gbm* R-package (Ridgeway, 2017), which are based on a machine-learning algorithm to build ensemble models by sequentially fitting regression trees from subsets of data. Processing time is relatively high for BRTs, and model overfitting can be more prevalent. However, BRTs implicitly include important interactions between variables and may have greater predictive power than GLMs or GAMs (Elith *et al.*, 2006). The settings for each BRT (number of trees, learning rate, and interaction depth) were optimized using tenfold cross validation repeated three times using the *caret* package (Supplementary Table S2; Kuhn *et al.*, 2018). The minimum number of observations in terminal nodes was set to ten.

With each of the above approaches, we developed separate models either for the probability of occurrence or for biomass. The probability of occurrence models was based on the presence and absence data and assumed a binomial error distribution. The biomass models used log-transformed biomass along with Gaussian errors for observations where biomass was greater than zero. To allow biomass models to include a larger range of environmental conditions, we added near-zero biomass values (1.0^{-10}) for each species for a fraction of hauls in survey regions where a species was never observed (Morley *et al.*, 2018). These near-zero values amounted to 10% of total observations or 10% of the total hauls in a region, whichever was smaller. As a result, all species projections could be conducted on an identical coast-wide scale and not just within environmental boundaries where a species has been historically observed. The use of near-zero values is similar to the "pseudoabsences" used in presence-only distribution models (Jones *et al.*, 2012). This approach assumes that climate variables are what restricts a species from a survey region. This assumption is supported by an analysis of global fish distributions showing that marine ectotherms generally fill their thermal niches (Sunday *et al.* 2012). Several species were observed in all survey regions on a given coast, so no near-zero values were added for these species (Table 1 and Supplementary Table S1). California market squid represented a unique case because two survey regions had fewer than three observations, so we also included near-zero values for those regions.

Final predictions of habitat suitability based on biomass models were calculated using a delta modelling approach, which uses the product of the predicted probability of occurrence and the exponentiated prediction of log biomass (Barry and Welsh, 2002). We emphasize that predictions of delta biomass in this context represent a relative value in habitat suitability and not actual future biomasses. In total, six niche models were fitted for each species, a probability of occurrence and a delta-biomass model for the GLM, GAM, and BRT approaches. Models were fit to the combined survey data from either the Pacific or the Atlantic (including the Gulf of Mexico) coasts, depending on the species. Predictor variables included seasonal SST and SBT based on a 3-month mean, annual minimum and maximum SBT that was based on the preceding 12 months, maximum SST, seafloor rugosity, sediment grain size, and a categorical indicator for ecological survey (Morley *et al.*, 2018). The categorical variable was included as an intercept term to account for differences in sampling gear and methodology between surveys.

To assess differences in predictive power among the six approaches, we fit a separate set of niche models using a training dataset that consisted of the initial 80% of hauls that occurred within each survey region. These training models were then used

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to compare predicted vs. observed values for the remaining 20% of the most recent data. Four metrics were used for comparison. First, for both probability of occurrence and delta-biomass models, we calculated mean annual values (i.e. mean of all hauls) for each survey with the testing data. Multiple annual values were calculated for survey regions where more than one season was sampled each year (Morley *et al.*, 2018). Linear regression was used to compare predicted vs. observed annual mean values, and associated R^2 values were used to compare the ability of niche models to represent large-scale patterns in species distribution.

The other three metrics for comparing niche model performance with independent test data only pertained to the probability of occurrence models and used the *dismo* R-package (Hijmans *et al.*, 2017). For these metrics, the modelled probability of occurrence was converted into a binary response (i.e. presence or absence), based on an estimated threshold value between 0 and 1. The kappa and true skill statistics (TSS; Allouche *et al.*, 2006) were calculated at all potential threshold values, and then, the maximum value for each of these metrics was recorded (i.e. kappamax and TSSmax; Elith *et al.*, 2006). Also, we calculated the area under the receiver operator curve (AUC). We chose these three threshold-independent statistics, which compute across a range of possible threshold values, because we ultimately modelled probability of occurrence and not a binary response for projections.

Projecting species habitat distribution

Output from 18 ESMs that participated in the Coupled Model Intercomparison Project 5 (CMIP5) was used to generate a range of ocean temperature change projections over the 21st century (Supplementary Table S3). From each ESM, we used output from simulations that were run under three future greenhouse gas emissions scenarios [i.e. Representative Concentration Pathways (RCPs)]: a "strong mitigation" (RCP 2.6), a "midrange mitigation" (RCP 4.5), and a "business as usual" scenario (RCP 8.5). These three scenarios represent roughly 1, 2, and 4°C of global mean atmospheric surface temperature change during this century, respectively (Collins *et al.*, 2013).

The ocean temperature projections used here represent an expanded version of the data set used in Morley *et al.* (2018). The additions were the RCP 4.5 scenario and two additional ESMs, which were treated identically to the projection data from the previous study. Briefly, we used the delta method to downscale ESM projections for the summer season (July–September). The delta values were added to a mean temperature climatology that was developed from the SODA3.3.1 data for 1995–2014. The climate projection grid (~0.25° latitude and longitude) was refined to 0.05° latitude and longitude based on the spatial resolution of the seafloor data (Figure 1). Depth of the projection grid was limited to 400 m or shallower. The resulting projection grid consisted of 65 826 individual cells on the Pacific coast, 69 209 on the Atlantic coast, and 13 383 in the Gulf of Mexico.

For each species, a set of 324 "baseline" projection time series (3 RCP × 18 ESM × 6 niche models) of annual-summer thermal habitat distributions from 2007 to 2100 was conducted (Figure 1). Annual grid cell values were aggregated by averaging projections within five 20-year bins, which were 2007–2020, 2021–2040, 2041–2060, 2061–2080, and 2081–2100. The baseline projections for each species are available in the Dryad Digital Repository, at https://doi.org/10.5061/dryad.44j0zpcbc. In addition to this set of baseline projections that used the original parameterized niche models, we conducted a second set of projections to quantify the role of parameter uncertainty within niche models. Examining parameter uncertainty was done by resampling parameter values for 40 iterations from a multivariate normal distribution, based on the variance of individual parameters in the GLMs or GAMs (Wong *et al.*, 2011; Degeling *et al.*, 2017), using the *MASS* package (Venables and Ripley, 2002). We did not include BRTs with this analysis, as they already represent an ensemble model and they could not be easily adapted to an analogous method for parameter resampling. Thus, using this method, we created 8640 projection time series (3 RCP × 18 ESM × 4 niche models × 40 parameter iterations) of annual thermal habitat distributions for each species, which were aggregated into 20-year bins as was done for the baseline projections (Figure 1).

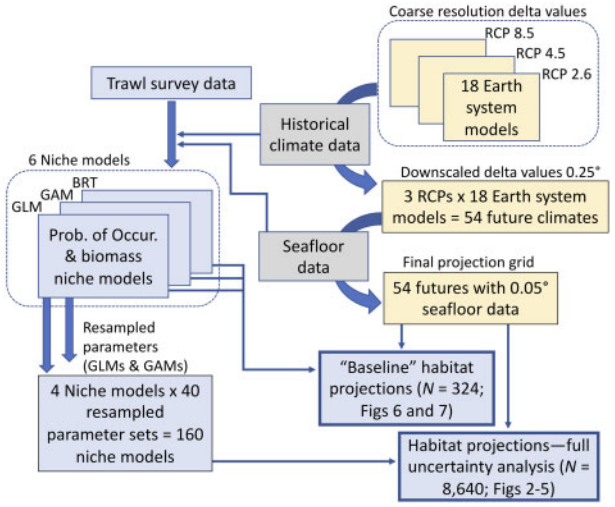

Figure 1. Modellingapproach used for each species to project shifts in habitat suitability and to quantify uncertainty among niche modelling approach, parameter uncertainty within niche models, RCP climate scenario, and climate simulation model. Biological data and models are in blue, static and historical environmental data are in grey, and projected climate data are in yellow.

Analyses

For each species, we summarized all of the projection time series by calculating the latitudinal centroid during each 20-year time interval, and also by calculating the percentage change in thermal habitat quantity during the 21st century. For both of these analyses, calculations were adjusted for grid cell area, which declines as latitude increases. Centroids were calculated as mean latitude, weighted by either delta biomass or probability of occurrence depending on the niche model (Pinsky *et al.*, 2013; Morley *et al.*, 2018). Centroids were calculated across the entire North American coastline, excluding the far-north, which was outside of our projection grid. Generally, changes in the centroid over time represent an effective way to quantify shifts in the modelled niche across the majority of a species' geographic range but do not provide information on changes in overall habitat quantity.

We analysed projections of thermal habitat quantity as a percentage change between the initial time period (2007–2020) and each future time interval. For each species, our analysis of habitat

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quantity was restricted to a northern and southern geographic region, which was done to examine how uncertainty varies regionally. The boundaries of these regions differed among species and—with the exception of market squid—were restricted to the US exclusive economic zone (EEZ).For all Pacific species except market squid, the northern region represented Alaskan waters and the southern region represented the west coast of the contiguous US. Market squid were similar to other Pacific species, but the northern region represented the EEZ of western Canada. For lobster, the northern region consisted of the Gulf of Maine and Georges Bank (east of −70° longitude) and the southern region represented the remaining US continental shelf north of Cape Hatteras, North Carolina (NC). For summer flounder and black sea bass, the northern and southern regions were divided by Cape Hatteras, NC and did not include the Gulf of Mexico. Average annual thermal habitat quantity was calculated as the sum of all projected delta biomass or probability of occurrence values from the northern and southern regions of the projection grid within each aggregated 20-year time interval (Morley *et al.*, 2018). From these habitat quantity values, we calculated percentage change from the initial time period. Our approach with habitat quantity contrasted somewhat with our analysis of centroid, which was not calculated as a percentage change or shift from the initial time period. The reason for using percentage change with habitat quantity analysis was to allow the niche models that projected the probability of occurrence to be analysed on the same scale as the delta-biomass models.

For each species, we quantified the sources of projection uncertainty during each future time period using general linear models

$$y \sim \mathrm{RCP} + \mathrm{ESM} + \mathrm{SDM} + (\mathrm{RCP} \times \mathrm{ESM} \times \mathrm{SDM}) + e_i,$$

where y is either the centroid or percentage change in habitat quantity for the northern or southern region for a given time period, SDM refers to the four different niche models used (not including BRTs), and residual error e indicates variation associated with the ith set of parameter values for a given SDM. To characterize uncertainty, we partitioned the sum of squares (SS) in the general linear models (Hare *et al.* 2012a, b). We used the proportion of the total SS that was explained by residual error to quantify parameter uncertainty. To partition the remaining SS (i.e. $SS_{total} - SS_{residual}$) among RCP, ESM, and SDM, we used dominance analysis (Azen and Budescu, 2003). Dominance analysis uses R^2 values from all possible model subsets to quantify the relative importance of each predictor variable.

Our examination of baseline projections (i.e. no resampling of parameter values) was used to compare niche models. We restricted our analysis of baseline projections to RCP 8.5 because this high-emission scenario had the most substantial changes in species distribution and more divergence among the niche models compared to RCP 2.6 and 4.5. To compare niche models, we calculated the ensemble mean and standard deviation of centroid and percentage change in habitat quantity across ESMs for each time period.

Ensemble projections across all ESMs and niche models (including BRTs) were also conducted using the baseline projections with RCP 8.5. To calculate the ensemble mean, we first needed to transform the projections based on delta-biomass niche models to match the scale of the probability of occurrence projections (i.e. range between 0 and 1) so that weighted means could be calculated across niche models. We used the following equation:

$$\mathrm{biomass}_{ijkl} = \log_{10}(\Delta\mathrm{biomass}_{ijkl}) / \max\left(\log_{10}(\Delta\mathrm{biomass}_{l})\right),$$

where rescaled delta-biomass in grid cell i, projection year j, ESM k, and niche model l is calculated as the log-transformed biomass divided by the grid cell with the highest log-projected value within projections for niche model l across all years and ESMs. The delta-biomass values were first log-transformed, because some species had a small number of grid cells with high biomasses and without a transformation these values were highly influential when projected biomass was rescaled and did not resemble observed biomass distributions within historical data. We then calculated the ensemble mean within each grid cell for the 2007–2020 and 2081–2100 time periods. This was done by first calculating weighted means across niche models within each ESM and time period, using R^2 values from mean survey–year relationships (Table 1) for weights. Then, means were calculated across ESMs for each grid cell and time period. The ensemble habitat projection map for 2007–2020 was compared with a map showing the change in habitat suitability for the end of the century. The scale of change was standardized to range between −1 and 1, where all values were proportional to the grid cell experiencing the greatest change (positive or negative). Finally, we calculated the standard deviation among ESMs in projected change in habitat suitability between the two time periods in each grid cell.

To examine how our projections for the present time period (2007–2020) resembled observations of species distributions, we plotted species occurrence records, which were taken from the Ocean Biogeographic Information System (OBIS) (Ocean Biogeographic Information System, 2019) and trawl survey data from the present study. For both datasets, we considered each record (i.e. unique date and location of a sample) as a single occurrence, because commercial fishery observer data are included in OBIS and can include large numbers of individuals per record. For some species, the OBIS data also contained trawl survey data from the present study, and when this occurred, we removed the duplicate data. Occurrence data were aggregated to a 0.25° latitude and longitude spatial grid and we plotted logged values to reduce the importance of heavily sampled areas (Supplementary Figure S1).

Results

Partitioning projection uncertainty

General patterns in the sources of uncertainty and amount of variation were evident for halibut (Figure 2), ocean perch (Figure 3), summer flounder (Figure 4), and lobster (Figure 5). In most cases, the total SS increased with projections that were farther into the future (Figures 2–5, panels a–c). One major reason for this was an increasing variance component for greenhouse gas emission scenario (i.e. RCP) towards the end of the century (e.g. Figures 2a and 4c). The amount of variation due to ESMs and niche model also tended to increase for projections that were later in the century (e.g. Figures 4b and 5b), but the increases were proportionally less than for RCP.

The increasing amount of uncertainty at later time periods was also evident in the distributions of projections by time period (Figures 2–5, panels d–f). For example, halibut and ocean perch

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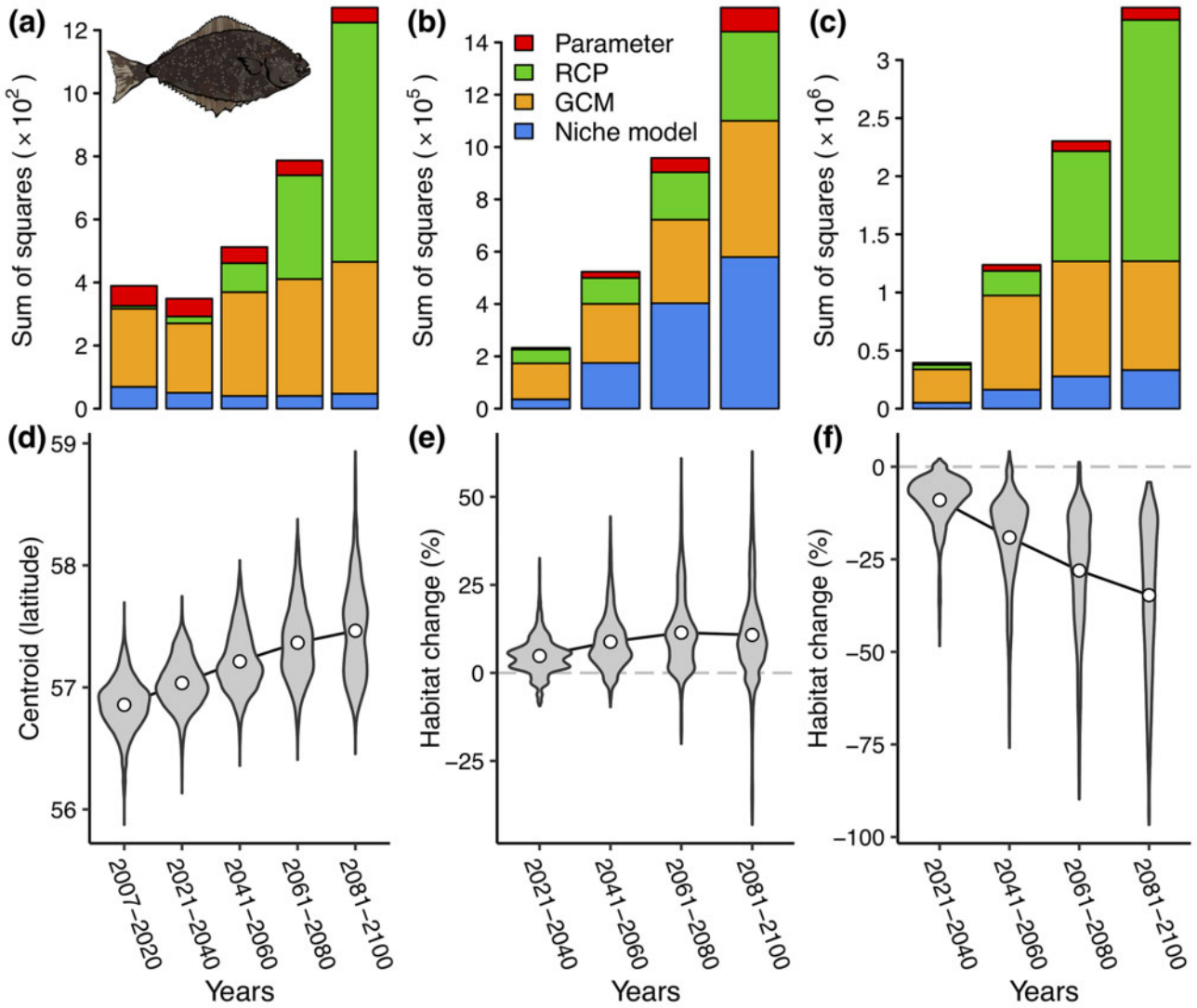

Figure 2. Sources of projection uncertainty for Pacific halibut *Hippoglossus stenolepis*. Partitioning of the sum of squares (a–c) with general linear models and distributions of projection results (d–f) by time period for latitudinal centroid (a, d), and percentage change in suitable habitat from the initial (2007–2020) time period for the northern region (b, e) and the southern region (c, f). Circles in (d)–(f) are mean values.

had relatively narrow ranges for southern habitat loss projections by 2021–2040, and both species had a prominent mode in the distribution of outcomes for this time period (Figures 2f and 3f). In contrast, for these two species at the end of the century, the distribution of projections was more evenly spread across almost a full range of negative outcomes from 0 to 100% loss. Indeed, long-tailed distributions were common among projections towards the end of the century, which indicated that more extreme outcomes occurred with certain combinations of RCP, ESM, and niche model.

There were some exceptions to the above patterns. For example, variation for the projected centroid of ocean perch was relatively stable throughout the 21st century, due to a reduction in variation among ESMs for later projections and little increase in variation among RCPs (Figure 3a). This pattern for ocean perch was due to more variation in projected southern habitat quantity among ESMs during the early 21st century. Similarly, market squid exhibited convergence in niche model centroid projections through time, leading to a general decline in SS (Supplementary Figure S3a). Another exception from the general patterns occurred for projections of the change in thermal habitat quantity for market squid and black sea bass (Supplementary Figures S3b and S4b and c). Both of these species had pronounced increases in the SS across niche models, ESMs, and RCPs towards the end of the century.

Two additional patterns across species were evident. First, parameter uncertainty was relatively unimportant compared to the other three factors examined (Figures 2–5). Second, projected centroids increased in latitude through time and northern thermal habitat quantities increased while southern habitat decreased, despite uncertainty (Figures 2–5, panels d–f). This pattern varied among species and, in some cases, projected changes stabilized towards the end of the century (e.g. Figures 2e and 3e). Some species showed less projected change over time, including mean

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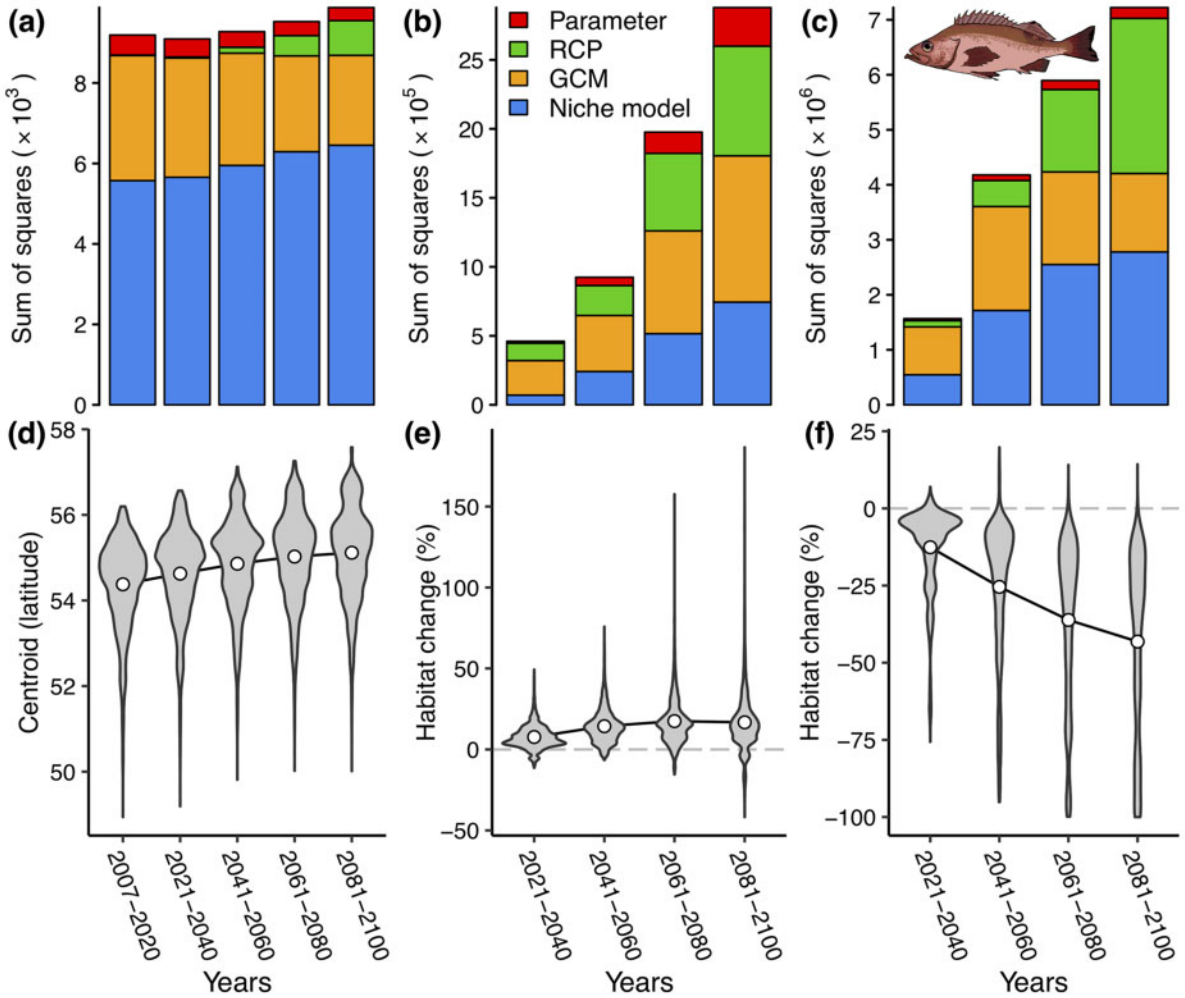

Figure 3. Sources of projection uncertainty for Pacific ocean perch *Sebastes alutus*. Partitioning of the sum of squares (a–c) with general linear models and distributions of projection results (d–f) by time period for latitudinal centroid (a, d) and percentage change in suitable habitat from the initial (2007–2020) time period for the northern region (b, e) and the southern region (c, f). Circles in (d)–(f) are mean values.

change in habitat quantity for lobster in their northern region (Figure 5e).

Within species, the characteristics of uncertainty varied depending on what metric was examined. For example, niche model contributed little to SS for halibut centroid projections, but for change in northern habitat quantity, niche model was more important than greenhouse gas emissions scenario (Figure 2a and b). Similar contrasts could be made for all seven species.

Niche model comparisons with RCP 8.5

All of the niche models that projected probability of occurrence performed well when tested with independent data (Table 1 and Supplementary Table S1). For example, AUC scores for all species and niche models were greater than 0.85. Furthermore, when examining survey–year relationships (i.e. mean of all hauls annually for each survey using independent data), all r^2 values were >0.47 (mean = 0.77). This suggests that at the spatial scales at which trawl surveys are conducted (e.g. Gulf of Alaska; southeast United States), the probability of occurrence niche models effectively represents variation in species distributions. The ability of the delta-biomass models to reflect survey–year variation in mean catch was more variable across niche modelling approaches than the probability of occurrence approach (mean $r^2 = 0.48$; Table 1 and Supplementary Table S1). For example, the GLM and GAM delta-biomass niche models for summer flounder performed poorly when predicting regional scale annual catch per unit effort (Table 1), but the BRT models for summer flounder were strongly related to observed values. These results underscore how much niche models can differ in performance. The predictive performance of delta-biomass models was not related to how much deviance was explained by biomass GAMs when comparing across species (Table 1 and Supplementary Table S1). In particular, biomass GAMs for species that included near-zero values during model fitting had a greater proportion of deviance explained due to the replicated-identical data points added to the margins of species' niche space.

For all species, there were important differences among the six niche modelling approaches for projecting centroid or percent

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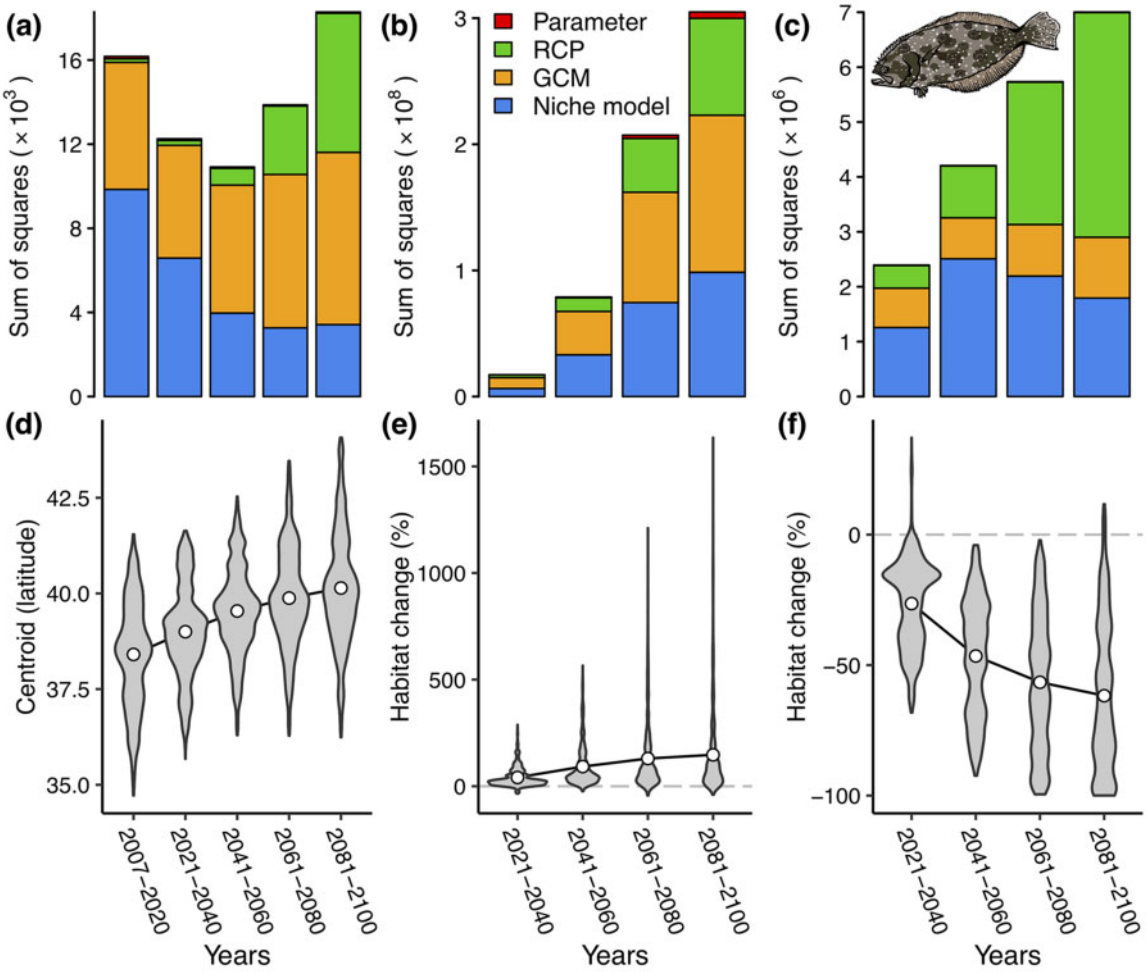

Figure 4. Sources of projection uncertainty for summer flounder *Paralichthys dentatus*. Partitioning of the sum of squares (a–c) with general linear models and distributions of projection results (d–f) by time period for latitudinal centroid (a, d), and percentage change in suitable habitat from the initial (2007–2020) time period for the northern region (b, e) and the southern region (c, f). Circles in (d)–(f) are mean values.

change in habitat quantity (Figure 6 and Supplementary Figure S5). Differences among niche models were apparent in both the mean projection values and the standard deviation among the ESM ensemble members. However, while niche models often varied in the magnitude of projected change, the overall direction of change was typically similar with only a few exceptions. For example, black sea bass had poor agreement among niche models in terms of percentage change in suitable habitat (Supplementary Figure S5f and i) and the more divergent niche models also had poor agreement among ESMs as indicated by the large standard deviations.

The projection trends for the niche models that were based on the probability of occurrence tended to cluster more closely together than the delta-biomass models (Figure 6 and Supplementary Figure S4). Furthermore, the delta biomass and probability of occurrence models often differed considerably within a modelling approach (i.e. GLM, GAM, and BRT; e.g. Figure 6f and g), although for some species the presence–absence and biomass models were similar within approaches (e.g. Figure 6i and j). Finally, of the six niche model approaches, the GLM delta biomass-based projections most commonly had results that differed substantially from other niche modelling approaches (e.g. Figure 6e and h, Supplementary Figure S5c and e). These instances of divergent projections based on GLM delta-biomass models were typically associated with high uncertainty among ESMs.

Ensemble projections with RCP 8.5

For all species, the ensemble projection for 2007–2020 (Figure 7 and Supplementary Figure S6) represented historical occurrence data well (Supplementary Figure S1). Some of the minor differences between the projected and observed distributions may be due to projected shifts in suitable habitat from the historical occurrence record. Also, the occurrence data were taken from all seasons, while our projections represent summer habitat. For example, summer flounder (Figure 7e) and black sea bass (Supplementary Figure S6e) are projected to be at higher densities nearshore in the mid-Atlantic region of the United States, but occurrence data occur from across the shelf and include overwintering habitat.

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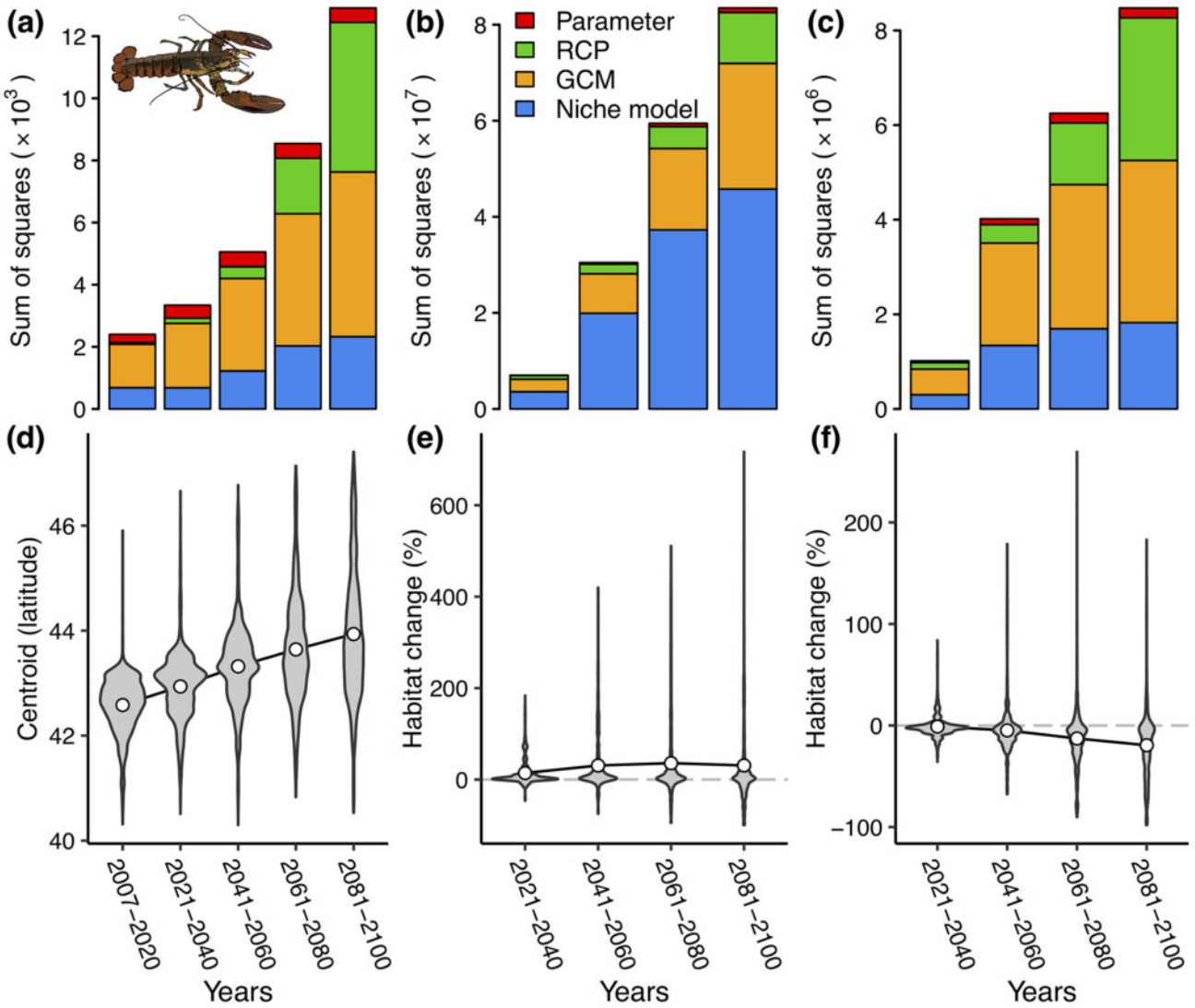

Figure 5. Sources of projection uncertainty for American lobster *Homarus americanus*. Partitioning of the sum of squares (a–c) with general linear models and distributions of projection results (d–f) by time period for latitudinal centroid (a, d), and percentage change in suitable habitat from the initial (2007–2020) time period for the northern region (b, e) and the southern region (c, f). Circles in (d)–(f) are mean values.

Under RCP 8.5, all species were projected to experience major declines in thermal habitat suitability over large areas of their southern distribution during the 21st century (Figure 7 and Supplementary Figure S6), with the exception of market squid, which had a mix of negative, neutral, and positive projections off of the southern west coast (Supplementary Figure S6d). Conversely, there were increases in habitat suitability at northern regions of species' present distributions and poleward shifts of the northern geographic range limits. The projected shift in thermal habitat for halibut and lobster was particularly severe, because much of their existing range for the 2007–2020 time period showed major declines in habitat suitability, suggesting the potential for near complete displacement into new geographic areas (Figure 7a and b and g–h).

An examination of the projection maps revealed several important subregional scale shifts in habitat. For example, while a majority of niche models for halibut and lobster showed a net neutral change in northern region habitat quantity (Figure 6e and h), there were significant shifts in habitat distribution. For halibut, a stark contrast existed between the Eastern Bering Sea where there was a gain in thermal habitat and the Gulf of Alaska and the Aleutian Islands where habitat suitability declined (Figure 7b). For northern region lobster (Figure 6h), thermal habitat shifted into deeper habitats within US EEZ waters and away from Georges Bank and coastal areas within the Gulf of Maine (Figure 7h and Supplementary Figure S6d).

The spatial distribution of projection uncertainty among ESMs was different for each species (Supplementary Figure S7), which reflects the unique way species' niche model ensembles interacted with ESMs. Generally, there was stronger agreement among ESMs in southern regions where species' habitat declined (e.g. Supplementary Figure S7b and c). Some species had high

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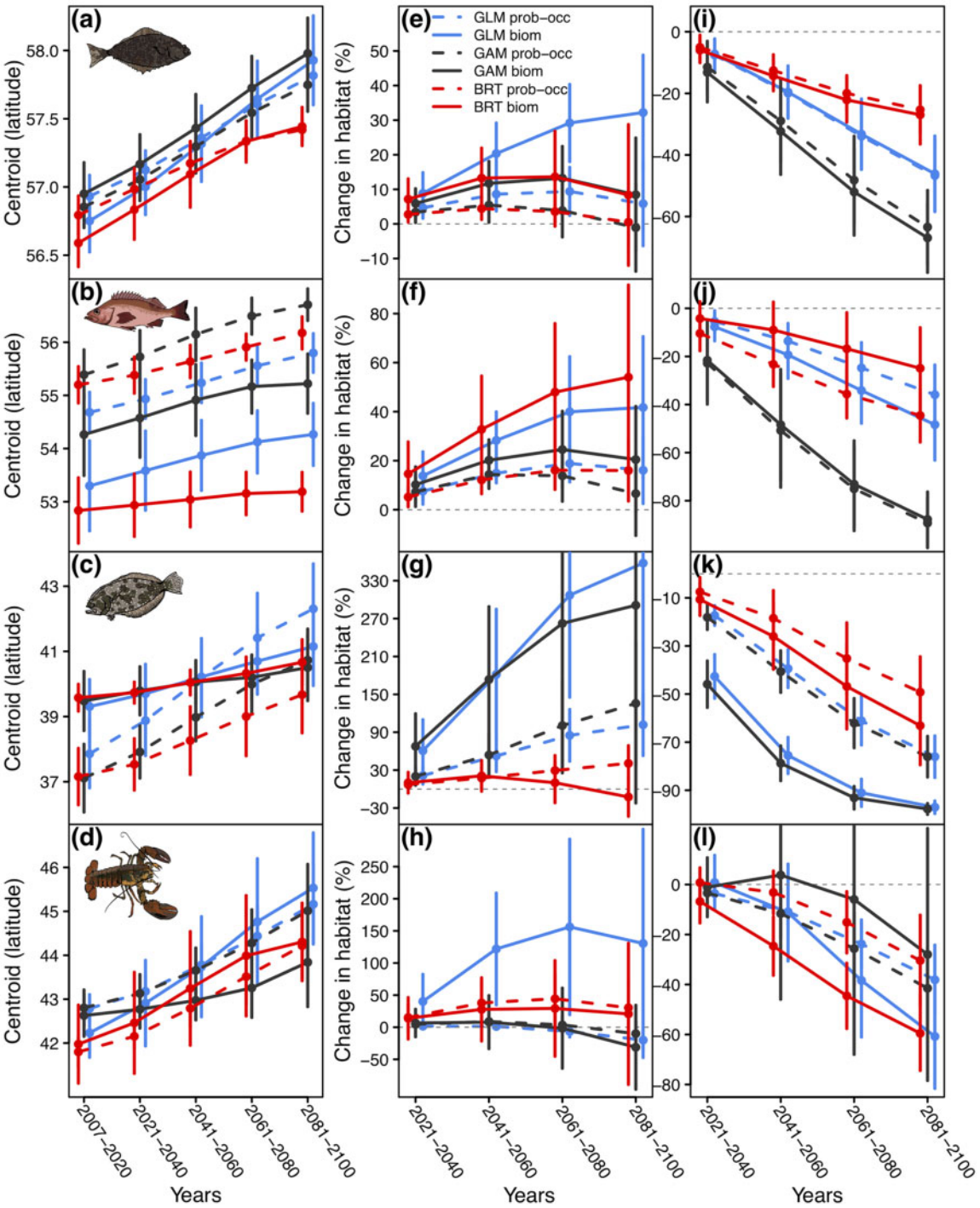

Figure 6. Ensemble mean projections for the RCP 8.5 scenario using six different niche models including generalized linear models (blue), generalized additive models (dark grey), and boosted regression trees (red) for the probability of occurrence (dashed line) or for delta biomass (solid line). Error bars are one standard deviation and represent uncertainty among 18 Earth system models. Columns represent mean latitudinal centroid (a–d), and percentage change in suitable habitat from the initial time period (2007–2020) in the northern (b, f, g, h) and southern (c, j, k, l) regions for Pacific halibut (a, e, i), Pacific ocean perch (b, f, j), summer flounder (c, g, k), and American lobster (d, h, l). Note that the full extent of error bars is not shown in (g) and (l).

variability among ESMs at their northern expanding range edge, including Pacific halibut and market squid (Supplementary Figure S7a and f).

Discussion

This study represents one of the most comprehensive examinations of uncertainty to date for the projection of species' habitat

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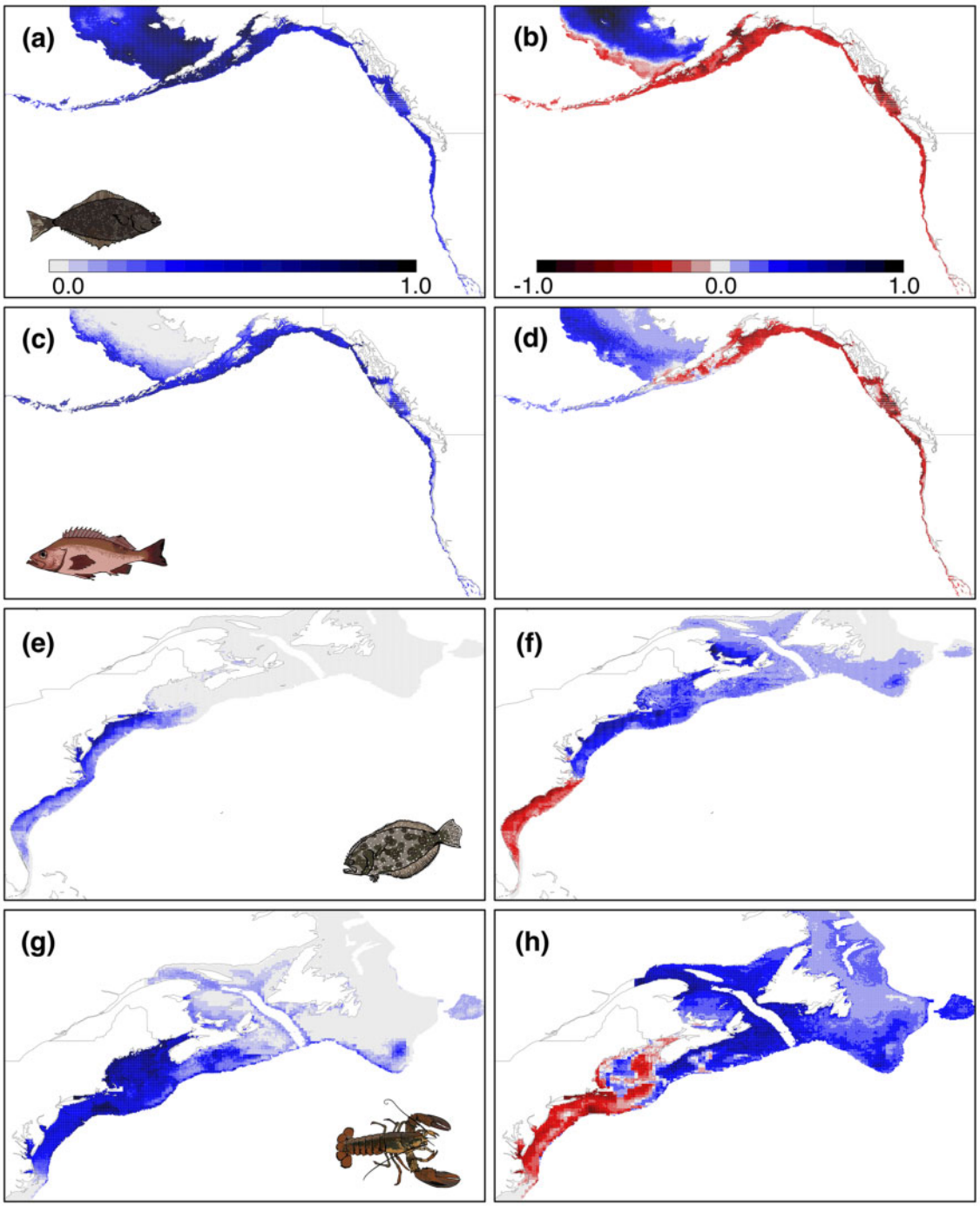

Figure 7. Ensemble mean projections across 18 Earth system models and 6 niche models for the RCP 8.5 scenario for Pacific halibut (a, b), Pacific ocean perch (c, d), summer flounder (e, f), and American lobster (g, h). For each species, the left panel shows projected suitable habitat for the initial time period of 2007–2020, and the intensity of the blue represents habitat suitability while grey represents areas of the projection grid that are not suitable. The right panels show projected change in habitat suitability between the 2081–2100 time period and 2007–2020. For the right panels, red represents a decline in habitat suitability, blue represents increases in habitat suitability, and grey represents areas of no change; increasing intensity of blue (red) represents a proportionally greater increase (decrease) in habitat suitability.

or distribution in the coming century. Generally, there has been an inadequate treatment of uncertainty with species projections (Planque *et al.*, 2011; Cheung *et al.*, 2016a; Freer *et al.*, 2018), even though a number of previous studies have included more limited—but still very useful—uncertainty analyses with projections of habitat (e.g. Thuiller, 2004; Hare *et al.*, 2012b; Jones and Cheung, 2015). We used 54 projections of future climate (3 RCPs × 18 ESMs) and within each of these futures we projected six niche modelling approaches, including unique sets of parameter values within four of these niche models that

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reflected the uncertainty in species habitat associations. We found major differences in projection uncertainty among species. This result is similar to previous work, which found that species vary in the relative amount of uncertainty in projected shifts in habitat based on the level of agreement among a suite of ESMs (Morley *et al.*, 2018). In the present study, we have expanded on previous work by showing that the sources of uncertainty differ among species. Furthermore, within each species, we found regional differences in uncertainty characteristics (i.e. north vs. south), and also differences between modelled responses (i.e. centroid vs. habitat quantity). Even pairs of species with similar present-day geographic ranges had major differences in uncertainty characteristics (e.g. summer flounder vs. black sea bass). This suggests that features of individual species niche models can interact in unique ways with climate projections.

Characterizing uncertainty in species projections

We examined four major sources of uncertainty in projecting species habitat shifts: greenhouse gas emission scenario, ESM, niche model, and parameter uncertainty. For greenhouse gas emissions, the relative importance of RCP scenario increased with projections on longer timescales, which is consistent with previous research (Hare *et al.*, 2012a, b; Goberville *et al.*, 2015; Thuiller *et al.*, 2019). This is due to ocean temperature projections from different RCPs becoming increasingly divergent throughout the 21st century. For example, by 2050, there is about a 0.5°C difference among RCPs in ensemble mean projections of global SST, but by the end of the century, SST projections for the RCPs 2.6 and 8.5 differ by around 2°C (Frölicher *et al.*, 2016). It follows that the magnitudes of projected shifts in habitat are strongly influenced by RCP scenario at the century scale (Cheung *et al.*, 2009; Morley *et al.*, 2018). In the present study, the uncertainty due to greenhouse gas emissions scenario was important for all species by the end of the century. Therefore, it is not surprising that the distributions of projection results spread out in later time periods (e.g. Figure 1f). However, for all species, there were projection metrics where RCP was not the most important source of uncertainty at the end of the century.

The suite of 18 ESMs used in this study represented an important source of projection uncertainty for all species. However, there was not a consistent pattern among species in the characteristics of ESM uncertainty. Furthermore, for a given species, ESM uncertainty may have been important for one metric, such as shifts in the centroid, but have relatively strong agreement when examining changes in habitat quantity. These results illustrate how projected climate conditions can vary significantly among ESMs at regional scales (i.e. northern vs. southern half of range; Frölicher *et al.*, 2016), which are the most relevant for anticipating climate change impacts on living resources (Stock *et al.*, 2011; Cheung *et al.*, 2016a). Thus, our results illustrate the importance of conducting ensemble projections, based on multiple ESMs, to avoid the over-interpretation of regional biases that may be associated with specific models.

A potentially important source of uncertainty that was beyond the scope of our analysis was internal variability inherent in the climate system (Stock *et al.*, 2011). Internal variability reflects variability associated with climate modes such as El Nino-Southern Oscillation or the Atlantic Multidecadal Oscillation, or natural variability on small spatial scales unrelated to climate modes. Our analysis assumes that variation among the 18 ESMs represents a more important source of projection uncertainty than internal variation within the climate system. Nevertheless, we recognize that internal variability can be important, or even dominant, at regional scales (Stock *et al.*, 2011; Cheung *et al.*, 2016a; Frölicher *et al.*, 2016; Freer *et al.*, 2018). Our projections were aggregated into 20-year time intervals, which may reduce the importance of inter-annual variation among ensemble members of each ESM. However, the role of internal variability in projection studies deserves more attention in future studies.

Similar to ESM uncertainty, niche model choice was important for all species projections and also varied in its contribution to uncertainty across modelled response metrics within each species. Other studies have also shown the importance of niche model selection in projecting species distribution (Thuiller, 2004; Diniz-Filho *et al.*, 2009; McHenry *et al.* 2019; Thuiller *et al.*, 2019). Buisson *et al.* (2010) conducted future projections of stream fish distributions in France and characterized uncertainty across the same four modelled components as our study. They found that choice of species distribution model was the dominant source of uncertainty. Therefore, we recommend that future studies also conduct projections using an ensemble of species distribution models, in addition to a suite of ESMs, to reduce bias in any one approach (Araujo *et al.*, 2011; Jones and Cheung, 2015).

While numerous projection studies have examined structural uncertainty from species distribution models (Thuiller, 2004; Diniz-Filho *et al.*, 2009; Buisson *et al.*, 2010; Jones and Cheung, 2015; McHenry *et al.* 2019), few have simultaneously compared niche models that project biomass with those that project probability of occurrence. We found important differences between these two approaches. For the majority of species analysed here, predictions based on the probability of occurrence were more accurate at projecting geographic distributions than the delta-biomass models, when applied to independent test data (Table 1 and Supplementary Table S1). Furthermore, projections of habitat from the probability of occurrence models for the 2007–2020 time period were often qualitatively more similar to expected distributions based on occurrence records. We found that projections with the delta-biomass method consistently resulted in more geographically restricted distributions of suitable habitat than the probability of occurrence models. In several cases, this restriction of habitat was unrealistic based on occurrence records and contrasted greatly with the probability of occurrence approach, which is surprising considering that the delta-biomass approach represents the product of the two model predictions. Therefore, the biomass component of the coupled delta-biomass niche modelling approach might have a disproportionate effect on projections for some species. Nevertheless, the delta-biomass approach was effective for multiple species, suggesting that for some species a probability of occurrence model can be overly inclusive of habitat.

Uncertainty in the parameter values of our niche models generally contributed little to variation in our projection output. Similarly, Buisson *et al.* (2010) examined parameter uncertainty by fitting multiple models to subsets of data and they found that the different model parameterizations had a relatively small impact on projection uncertainty. The relatively small contribution of parameter uncertainty may be due to our use of niche models with multiple environmental predictors, and thus no single habitat feature determined a species distribution. Support for this conclusion comes from projections that are based on mechanistic distribution models, which are based on more specific aspects of

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a species' niche and thus might be more sensitive to parameter values (Pacifici *et al.*, 2015). For example, Hare *et al.* (2012b) showed that a majority of projection uncertainty for grey snapper range expansion along the southeast US coast was due to error around estimates of low-temperature tolerance.

Projected shifts in habitat for important resource species

All of the species analysed in this study are of economic importance to US fisheries, and a majority of them are also important in Canada. Under a high greenhouse gas emissions future, all seven species were projected to experience major northward shifts in suitable habitat, which will pose challenges to fisheries governance as these resources shift across jurisdictional boundaries (Pinsky *et al.*, 2018). The three Atlantic species included in our analysis have already experienced major range shifts and for two of these species—black sea bass and lobster—recent shifts have been linked to changes in ocean temperatures (Bell *et al.*, 2015; Le Bris *et al.*, 2018). The Atlantic region of the North American shelf contains some of the most rapidly increasing areas of ocean temperatures globally (Thomas *et al.*, 2017), which has led to relatively large distribution shifts among marine species in that region (Nye *et al.*, 2009; Pinsky *et al.*, 2013). Interestingly, the drivers of historical shifts in summer flounder distribution have been difficult to identify and have not been attributed to temperature (Bell *et al.*, 2015; Perretti and Thorson 2019). While more research is clearly needed on the mechanisms behind summer flounder shifts, we still believe that our projections for this species are valuable. In particular, our regional impact projections (i.e. north vs. south regions) were conducted at a broad geographic scale and historical shifts have largely occurred within our defined "northern" region for summer flounder (Perretti and Thorson 2019).

Recent historical shifts in resource species have already challenged existing management regulations and have led to conflict over regional allocation (Gaichas *et al.*, 2016; Dubik *et al.*, 2019) and also major changes in fishermen behaviour and fleet characteristics (Pinsky and Fogarty, 2012; Young *et al.*, 2019). Projections for shifts in habitat suggest that these challenges to management will only become more common in the 21st century in all regions of coastal North America (Morley *et al.*, 2018). Even under a strong mitigation scenario for greenhouse gas emissions, we can still expect significant surface ocean warming during the first half of the 21st century (Frölicher *et al.*, 2016). Furthermore, the probability of an ocean warming scenario consistent with RCP 2.6 may be low (Raftery *et al.*, 2017). Thus, the development of more climate-adaptive fisheries management frameworks is critical (Pinsky *et al.*, 2018). Species projections, such as the ones in this study, are immediately relevant to management efforts and can be incorporated into existing risk assessment frameworks (Gaichas *et al.*, 2016), species vulnerability reports (Hare *et al.*, 2016), and as objective negotiation tools for reallocation strategies (Dubik *et al.*, 2019). The projections in suitable habitat for the seven species in this study serve to illustrate some of the challenges to fisheries governance that are likely to occur.

The lobster fishery in the United States is of high-economic importance. Our projections for this species under RCP 8.5 can be compared with a population dynamics model used to project lobster population size at mid-21st century, which included fishery, ecosystem, and climate effects (Le Bris *et al.*, 2018). For the southern portion of the lobster geographic range—where the stock is presently depleted—our results for lobster projections are in agreement with Le Bris *et al.* (2018) and suggest that future climate change will inhibit recovery of the fishery to historic levels. In the northern region, Le Bris *et al.* (2018) also project declines in the population due to a reduction in recruitment and increased predation on juveniles, which were not factors included in our niche modelling approach. Our projections for the northern region of lobster within US waters differ somewhat from Le Bris *et al.* (2018) because a majority of our niche models projected either a small increase in habitat quantity or a zero net change by mid-century. However, our ensemble projection showed that nearshore habitat, which is important for lobster reproduction and recruitment, is projected to decline in habitat suitability. Furthermore, our results suggest that lobster may shift into deeper waters within the Gulf of Maine. Considering that ocean acidification is also expected to have a negative impact on this species (Fay *et al.*, 2017), lobster appear to represent a priority fishery to develop policy that mitigates economic loss to the region.

Other species in our analysis are projected to have major negative impacts from climate change within areas of important fishery investment. For instance, black sea bass are one of the most commonly targeted species for bottom-line commercial fisherman in the southeast United States (MacLauchlin, 2018). Our projections for black sea bass suggest that the dynamics of this multi-species fishery may dramatically change as habitat becomes less suitable for this key species. On the Pacific coast, shifts in sablefish and halibut distribution out of areas of historic abundance would also pose important challenges to fisherman and resource managers. The management challenges that are associated with shifting populations will be compounded by the potential for stocks to become less productive and more vulnerable to overfishing in regions of declining habitat quality (Bell *et al.*, 2018; Le Bris *et al.*, 2018).

Preparing for emerging fisheries will also be an important aspect of climate-adaptive resource management. For example, our projections suggest that suitable habitat for market squid will expand throughout the Gulf of Alaska. While such opportunities may help offset economic loss from other fisheries, it will be important for resource managers to regulate new fisheries conservatively as there is often a lack of critical data to assess stocks at their expanding edge (Pinsky and Mantua, 2014; Pinsky *et al.*, 2018). These uncertainties were taken into consideration when the multi-nation moratorium on arctic fishing was established (Hoag, 2017). It is noteworthy that several of the Pacific species analysed in our study have the potential to shift northward and off our projection grid. In particular, halibut have been projected to expand into the Arctic during the 21st century under RCP 8.5 (Wisz *et al.*, 2015).

Conclusion

Projections of climate change impacts on natural resources will probably become more available to resource managers in the near future. There are also a number of promising developments in this field that may refine projections of marine resources and create new opportunities, including high-resolution ocean models that better represent shallow areas of the continental shelf and that resolve mesoscale eddies (e.g. Saba *et al.*, 2016). Such high-resolution climate data will also enhance our ability to include additional niche dimensions, such as salinity and indicators of ocean currents, which were not included in the present analysis

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(McHenry *et al.* 2019). Furthermore, ensemble climate projections may be refined using model weighting techniques that are based on regional performance (Eyring *et al.*, 2019). The development of species projections based on other approaches to characterize biological responses, such as population dynamics models (Le Bris *et al.*, 2018), ecosystem models that include fishing impacts (Lotze *et al.*, 2019), and species distribution models that better account for survey and spatial autocorrelation effects (Perretti and Thorson 2019; Brodie *et al.*, 2020), may help quantify direct mechanisms behind climate impacts and also incorporate other potential constraints on species distributions.

The results from our uncertainty analysis are applicable to many forms of climate impact projection studies and serve to illustrate the importance of key deficiencies among projection studies (Planque *et al.*, 2011; Cheung *et al.*, 2016a). First, while greenhouse gas emission scenario is an important source of variation for long-term projections, other sources of uncertainty can remain important even when projecting at the century scale. Second, conducting projections with a suite of ESMs and species distribution models is critical, because individual ESMs can interact with species temperature preferences in complex ways at regional scales. In addition, broad distributions of projected outcomes were common. Thus, climate impact projection studies that are based on few ESMs or a single type of niche model may not effectively quantify the amount of uncertainty around results. Third, projections from different types of niche model can vary substantially. We found that basing projections on an ensemble of niche modelling approaches, which are weighted based on predictive performance with independent data, can be an effective and subjective method to project climate impacts on habitat. Finally, the dominant sources of uncertainty differed among species, and for most species, the uncertainty characteristics varied within different geographic regions.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling, which was responsible for CMIP5, and we thank the climate modelling groups for producing and making available their model output. For CMIP5, the US Department of Energy's Program for Climate Model Diagnosis and Intercomparison provided coordinating support and led development of software infrastructure in partnership with the Global Organization for Earth System Science Portals.Species graphics were created by Abigail Poray. We thank four anonymous reviewers for providing helpful comments on this manuscript.

Funding

Funding was provided by the Pew Charitable Trusts (# 28295), the Mid-Atlantic Fishery Management Council, the National Oceanic and Atmospheric Administration's "FY14 Understanding Climate Impacts on Fish Stocks and Fisheries to Inform Sustainable Management" initiative (Competition OAR-CPO-2014-2004106), US National Science Foundation (# OCE-1426891 and # DEB-1616821), and the Cooperative Institution for the North Atlantic Region (CINAR) under (NA14OAR4320158). JWM was supported by North Carolina Sea Grant (projects: R/18-SFA-2; 2016-R/16-HCE-3) and the North Carolina Policy Collaboratory. TLF acknowledges support from the Swiss National Science Foundation (PP00P2_170687) and the European Union's Horizon 2020 research and innovation programme (820989) (project COMFORT, Our common future ocean in the Earth system—quantifying coupled cycles of carbon, oxygen, and nutrients for determining and achieving safe operating spaces 30 with respect to tipping points).

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