





Predicted shifts of groundfish distribution in the Eastern Bering Sea under climate change, with implications for fish populations and fisheries management

Christopher N. Rooper ^{1*}, Ivonne Ortiz², Albert J. Hermann^{2,3}, Ned Laman⁴, Wei Cheng^{2,3}, Kelly Kearney ², and Kerim Aydin⁵

¹Pacific Biological Station, Fisheries and Oceans Canada (DFO), 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada

²Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA 98195, USA

³Ocean Environment Research Division, NOAA/PMEL, Seattle, WA 98195, USA

⁴Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, NMFS, Seattle, WA 98115, USA

⁵Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, NMFS, Seattle, WA 98115, USA

*Corresponding author: tel: +1 (250) 756-7050; e-mail: chris.rooper@dfo-mpo.gc.ca.

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Climate-related distribution shifts for marine species are, in general, amplified in northern latitudes. The objective of this study was to predict future distributions of commercially important species in the eastern Bering Sea under six climate scenarios, by incorporating predictions of future oceanographic conditions. We used species distribution modelling to determine potential distribution changes in four time periods (2013–2017, 2030–2039, 2060–2069, and 2090–2099) relative to 1982–2012 for 16 marine fish and invertebrates. Most species were predicted to have significant shifts in the centre of gravity of the predicted abundance, the area occupied, and the proportion of the predicted abundance found in the standard bottom trawl survey area. On average the shifts were modest, averaging 35.2 km (ranging from 1 to 202 km). There were significant differences in the predicted trend for distribution metrics among climate scenarios, with the most extensive changes in distribution resulting from Representative Concentration Pathway 8.5 climate scenarios. The variability in distributional shifts among years and climate scenarios was high, although the magnitudes were low. This study provides a basis for understanding where fish populations might expand or contract in future years. This will provide managers' information that can help guide appropriate actions under warming conditions.

Keywords: Alaska, climate change, demersal fish, fish habitat, generalized additive modelling, regional ocean model systems, species distribution modelling, trawl surveys

Introduction

Climate warming will generally have a more pronounced impact (increased air and sea surface temperature and loss of sea ice) at high latitudes (Alexeev *et al.*, 2005; Serreze *et al.*, 2009; Pithan and Mauritsen, 2014). Warming has already resulted in

distribution shifts for various marine species (Poloczanska *et al.*, 2013; Christiansen *et al.*, 2016; Dalpadado *et al.*, 2016; Pinsky *et al.*, 2018), but the magnitude of these shifts has varied from region to region even at high latitudes (Perry *et al.*, 2005; Mueter and Litzow, 2008; Kjesbu *et al.*, 2014; Kleisner *et al.*, 2017).

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Impacts of changing fish distributions can disrupt commercial fisheries, as species may move into new management jurisdictions where existing management frameworks do not have enough flexibility to respond to increased or new fish stocks (Dubik *et al.*, 2019). Conversely, the movement of fish stocks out of existing management areas can violate key management assumptions and reduce the amount of fish available in their historical commercial fishing grounds (Pinsky and Fogarty, 2012).

Species distribution modelling has been widely used to predict the effects of changing climate on the distributions of fish and invertebrates (Collie *et al.*, 2008; Lucey and Nye, 2010) and to detect the trajectories and velocities of climate change effects (Pinsky *et al.*, 2013). Recently, species distribution models have been developed for eastern Bering Sea (EBS) groundfish and invertebrate species (Sigler *et al.*, 2014; Rooper *et al.*, 2016; Laman *et al.*, 2018) and were used to define their essential fish habitat (EFH; “those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity”; NMFS 2010). Some of the modelled relationships, such as the relationship between bottom temperature and Kamchatka flounder (*Atheresthes evermanni*) catch, indicated that as temperatures warm catches will decrease. These models of environmental effects on catch can be used to predict changes in species distribution with changing environmental conditions.

The environmental conditions in the EBS are predicted to change over the next century according to projections from the Regional Ocean Modeling System for the Bering Sea (hereafter Bering10K). Dynamically downscaling regional future projections for Alaska’s EBS under multiple climate models and emission scenarios show a trend to warmer temperatures and a retreat of ice in the southeastern Bering Sea (Hermann *et al.*, 2013, 2016, 2019). These hindcasts capture key environmental features, such as the cold pool (Hermann *et al.*, 2016), an area where bottom water temperatures between 0 and 2°C persist through spring and summer after sea ice retreat (Wyllie-Echeverria and Wooster 1998). The cold pool has previously been shown to have a large influence on fish distributions in the EBS (Mueter and Litzow, 2008; Boldt *et al.*, 2012; Nichol *et al.*, 2019).

The objective of this project was to predict the future distributions of commercially important species in the EBS under six climate scenarios, by incorporating bottom temperature and current projections of the Bering10K model into species distribution models. The species distribution models were developed from annual summer bottom trawl survey data from 1982 to 2017 and are currently used to define EFH in the EBS (Laman *et al.*, 2017; Laman *et al.*, 2018). Climate scenarios are presented in decadal averages for three future time periods: (i) early mid-century, 2030–2039, (ii) late mid-century 2060–2069, and (iii) end of century: 2090–2099. The resulting predicted future fish distributions were then used to evaluate potential effects on EFH and to anticipate where shifts in distribution out of (or in to) the survey area may be perceived as changes in overall abundance of the stocks.

Material and methods

Study area

The effects of climate change on fish distribution were modelled for the EBS shelf ecosystem (Figure 1). This area extends northwards along the Alaska coast from the Aleutian Islands, Alaska Peninsula, and Bristol Bay to the Bering Strait in the north and is

bordered in the northwest by the US–Russia Convention Line. The EBS shelf is broad and flat extending ~200 km from shore at depths from 0 to ~200 m and is composed mostly of soft unconsolidated sediments (Smith and McConnaughey, 1999; Goddard *et al.*, 2016; Rooper *et al.*, 2016). The shelf break is typically at ~200 m depth, except in Bering Canyon where the shelf break is deeper (Sigler *et al.*, 2015). The northern Bering Sea (Figure 1) is shallow (mean depth <50 m) and also composed of unconsolidated sediments (Grebmeier *et al.*, 1988). The southern EBS shelf is commonly divided into three domains based on bathymetry and oceanographic fronts. These are the inner shelf (0–50 m), middle shelf (50–100 m), and outer shelf (100 m to the shelf break, Coachman, 1986).

Data used to model current fish distributions (1982–2012)

Summer bottom trawl surveys conducted by the Alaska Fisheries Science Center, Resource and Conservation Engineering Division on the EBS shelf and northern Bering Sea were used in these analyses (Figure 1). The EBS shelf summer bottom trawl survey data have been annually collected from a regular 20 × 20 nautical mile (nm) grid since 1982 (Conner and Lauth, 2017) covering the areas roughly south of 61°N. In 2010 and since 2017, this grid has been extended northwards to the Bering Strait to include both the northern Bering Sea and Norton Sound (Stevenson and Lauth, 2019). The subset of the EBS shelf survey area that includes the inner, middle, and outer shelf only is known as the standard survey area (Figure 1). In both of these surveys, the same vessels, trawl nets, and methodologies were used. All fishes and invertebrates caught during a survey bottom trawl haul were sorted to species or into broader taxonomic groups and their total weight and number in the catch were determined. The species examined in this study include only the most common and commercially valuable fishes and invertebrates caught in the EBS surveys (Table 1). In some cases, changes in taxonomy, such as the description of two species of rock sole (northern, *Lepidopsetta polyxystra*, and southern, *L. bilineata*) in 2001 from what was previously considered a single species (Orr and Matarese, 2000) necessitated using a subset of the time series of survey data (Table 1). Bottom trawl catches from survey hauls were converted to swept-area estimates of catch-per-unit-effort (CPUE) by weight using measurements of the distance travelled during the on-bottom portion of each tow and the measured (or estimated) net width (Conner and Lauth, 2017). Start and end positions for the vessel during the on-bottom portion of the trawl haul were collected using a GPS receiver on the vessel or LORAN positions prior to 1990. Vessel position was corrected to the position of the bottom trawl by triangulating how far the net was behind the vessel (based on the seafloor depth and the wire out) and subtracting this distance from the vessel position in the direction of travel of the bottom trawl haul. The mid-point of the trawl path between the start and end positions was used as the location of the tow. The longitude and latitude data for each tow (and all other geographical data including the raster layers described here) were projected into Alaska Albers Equal Area Conic projection (standard parallels = 55 and 65°N and centre longitude = 154°W).

Six independent variables [depth, slope, maximum tidal current, sediment grain size (ϕ), bottom current, and bottom temperature] were used to predict the distribution of fish and invertebrates in the EBS (Table 2). These variables were chosen

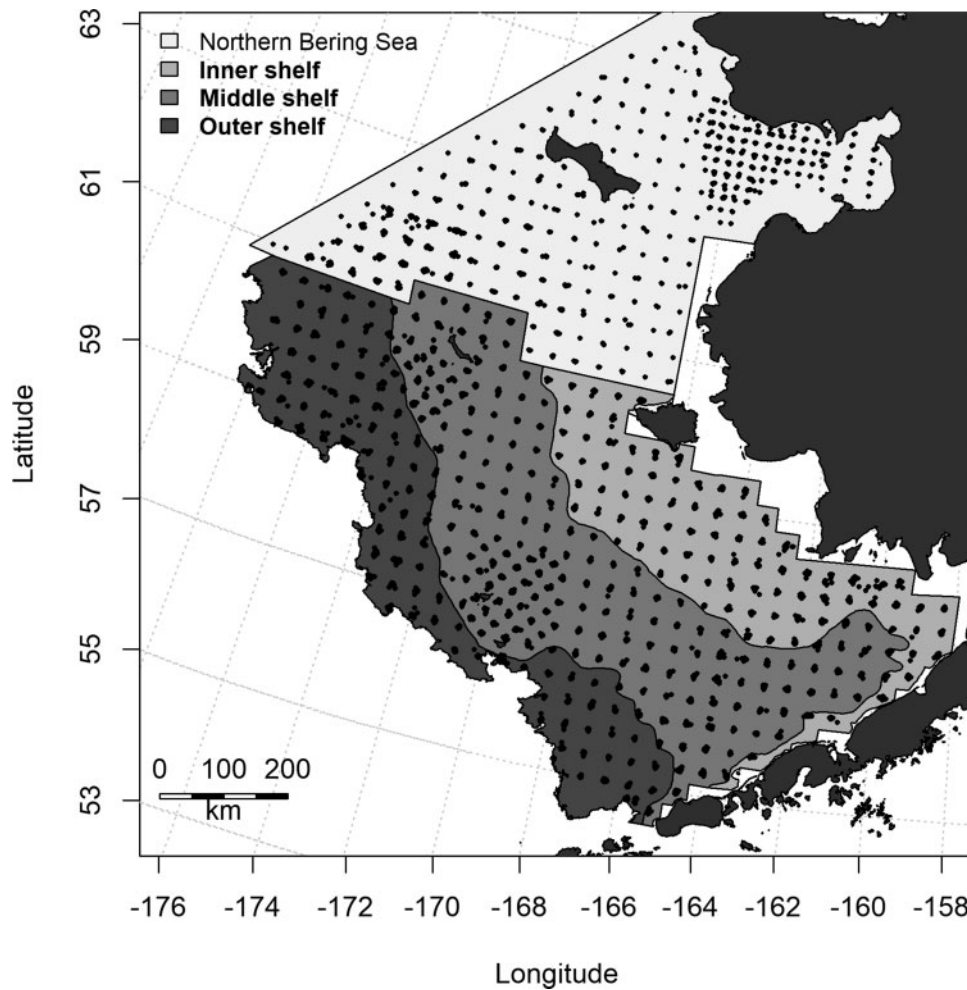


Figure 1. Map of eastern Bering Sea showing summer bottom trawl stations from 1982 to 2017. Polygons depict the outer (~100–200 m depth), middle (50–100 m depth), and inner shelf (0–50 m depth) and comprise the area of the standard EBS shelf survey that has been sampled every year since 1982 (indicated by bold legend text). The Northern Bering Sea was also surveyed completely using the same gear methods in 2010 and 2017. The longitude and latitude data for each tow (and all other geographical data) were projected into Alaska Albers Equal Area Conic projection (standard parallels = 55 and 65°N and centre longitude = 154°W).

Table 1. List of species and survey years used to model eastern Bering Sea future habitat conditions, along with maximum temperature (°C) where the species was recorded during eastern Bering Sea shelf bottom trawl surveys.

Species	Years modelled	Maximum temperature adults (°C)	% positive catches—juveniles	% positive catches—adults	Max. juvenile length (cm)
Alaska plaice, <i>Pleuronectes quadrituberculatus</i>	All	11.7	–	55.24	28
Arrowtooth flounder, <i>Atheresthes stomias</i>	1993–	7.6	34.08	40.63	35
Flathead sole, <i>Hippoglossoides elassodon</i>	All	9.8	49.99	65.8	25
Northern rock sole, <i>Lepidopsetta polyxystra</i>	2001–	9.9	32.75	46.47	24
Pacific cod, <i>Gadus macrocephalus</i>	All	9.9	72.72	80.28	46
Walleye pollock, <i>Gadus chalcogrammus</i>	All	11.7	68.35	84.72	25
Red king crab, <i>Paralithodes camtschaticus</i>	1996–	9.6	–	21.19	–
Snow crab, <i>Chionoecetes opilio</i>	All	7.2	–	68.76	–
Tanner crab, <i>Chionoecetes bairdi</i>	All	8.7	–	59.17	–
Yellowfin sole, <i>Limanda aspera</i>	All	11.7	54.08	61.37	25

The percentages of positive catches for the data analysed (1982–2017, $n = 14\ 107$) are shown for juveniles and adults and the length used to divide the two stages. Bold text indicates the modelling of CPUE data used a lognormal distribution, while regular text indicates the modelling used a Tweedie distribution.

Table 2. Definitions, sources, and interpolations methods for explanatory variables used to model fish and invertebrate distributions in the eastern Bering Sea under climate change scenarios.

Variable	Unit	Definition	Interpolation method	Source
Depth	m	Depth of bottom trawl haul and bathymetry of the seafloor based on digitized and position corrected National Ocean Service charts	Linear interpolation	Bottom trawl survey data (Prescott and Zimmermann, 2015); S. Lewis, Alaska Regional Office, NMFS, Anchorage, Alaska
Slope	%	Maximum difference between a depth measurement and its adjoining cells	–	Derived from depth raster
Maximum tidal current	cm s ⁻¹	Maximum of the predicted tidal current at each bottom trawl location over a 1-year cycle	Ordinary kriging	Egbert and Erofeeva (2002)
Sediment grain size (phi)	–	Sediment grain size derived from historical bottom sampling in the eastern Bering Sea compiled in the EBSED database	Ordinary kriging	Richwine et al. (2018)
Mean bottom current	m s ⁻¹	Ocean current speed predicted from the Bering10K model during years 1982–2012 and averaged on a 10 km × 10 km grid	Inverse distance weighting	Hermann et al. (2013)
Bottom temperature	°C	Seafloor temperature predicted from the Bering10K model during years 1982–2012 and averaged on a 10 km × 10 km grid	Inverse distance weighting	Hermann et al. (2013)

based on their importance in determining fish distributions from previous analyses of EBS trawl survey data (e.g. McConnaughey and Smith, 2000; Sigler et al., 2015; Laman et al., 2018) and the details of the variable construction and maps of their distribution are found in [Supplementary Material S1](#). A key difference between the variables used for modelling here and the modelling conducted by Laman et al. (2018) is the removal of spatial variables (latitude and longitude) from the present analysis. These two variables were removed for two reasons, first to reduce the potential for a stationary effect of spatial location on the distribution of fishes in the future and second because the strong latitudinal and longitudinal gradients in depth and sediment size on the eastern Bering Sea shelf were strongly correlated with the spatial terms. All analyses were conducted using R software (R Core Team, 2019).

Generalized additive modelling methods and model validation

Generalized additive models (GAMs; Hastie and Tibshirani, 1986; Hastie and Tibshirani, 1990) implemented in the mgcv package (Wood, 2006) were used to parameterize relationships between fish and invertebrate CPUE and habitat variables (e.g. Laman et al., 2018). The raw or log-transformed CPUE data (including zero catches) were the dependent variable in the analyses. For each of the habitat variable, the basis degrees of freedom used in the smoothing function were constrained to ≤ 3 to reduce overfitting of the GAMs. The full model was expressed as:

$$y = s(\text{depth}) + s(\text{slope}) + s(\text{grain size}) \\ + s(\text{maximum tidal speed}) + s(\text{current speed}) \\ + s(\text{temperature}) + \epsilon,$$

where y was the dependent variable (raw or log-transformed CPUE) and s indicates a thin plate regression spline smoothing function (Wood, 2006). For ten fish and invertebrates that exhibited a large degree of zero-inflation ($\geq 66\%$ of the observations

were zeros; Table 1), raw CPUE data and a Tweedie error distribution (Tweedie, 1984) were used for model fitting (Dunn and Smyth, 2005; Wood et al., 2016). The Tweedie power parameter was fit simultaneous with the GAM parameters and by default restricted to a range from 1 to 2 to best represent a compound Poisson distribution with non-negative values and a high degree of zero-inflation. For the remaining six fish and invertebrates with high proportions of positive catches, CPUE was log-transformed (with the addition of half the minimum positive catch) prior to modelling. Backward stepwise elimination was used to remove non-significant variables. Initially a full model containing all independent variables was fit to the data. Then, the least significant variable was removed from the model, provided it had $p > 0.05$, the generalized cross-validation (GCV) score was lower with the elimination of the variable, and the estimated degrees of freedom of the variable was not equal to 1 (Weinberg and Kotwicki, 2008). The resulting reduced model was re-fit to the data. Stepwise variable removal was continued until all variables were significant in the model or removal of additional variables resulted in a higher GCV score. The remaining variables in the best model were determined to have significant effects on the CPUE of that species.

We did not include latitude or longitude to evaluate habitat characteristics irrespective of location; however, analyses were undertaken to explore significant spatial autocorrelations that were present in the residuals of the models. Spatial autocorrelation in the residuals is primarily important due to the assumption of independence among the observations and the impact that spatial dependence can have on the realized sample size. For all species, there was some level of significant spatial autocorrelation measured by Moran's I (Moran, 1950) and spatial patterns in the residuals are shown in [Supplementary Material S2](#). Three methods were used to reduce and evaluate the effects of this autocorrelation on the results, including a smoothed bivariate term of latitude and longitude in the initial GAM formula, implementation of a variable coefficients GAM (Bartolino et al., 2011), and

treating geographic position as a random effect in a generalized additive mixed model (Wood, 2006). While each of these approaches reduced the Moran's I statistic, the spatial autocorrelation in the residuals remained at significant levels ($p < 0.001$). Because the primary concern of this modelling was to make predictions regarding future distributions and because of the previously discussed concerns about including stationary variables in the analyses, we ignored the effects of spatial autocorrelation in the residuals, as such the significance levels for variables in the GAM model are likely overestimated (due to a smaller realized sample size for the CPUE data) and should be regarded with some caution.

Predicting future fish distributions (2013–2099)

Predictions of future conditions for the bottom temperature and bottom current speed variables were available from Bering10K model projections driven by six climate scenarios. The scenarios were driven using global General Circulation Model (GCM) output from the Intergovernmental Panel on Climate Change (IPCC) sponsored Coupled Model Intercomparison Projects, version 5 (CMIP5). The models used were GFDL-ESM2M, CESM, and MIROC, under Representative Concentration Pathways (RCPs) 4.5 and 8.5 (Hermann *et al.*, 2019), for a total of six climate scenarios. These downscaled global climate models were previously found to perform well for the EBS (Wang *et al.*, 2012) based on their ability to capture decadal variability (e.g. the Pacific Decadal Oscillation) and ice dynamics (Wang *et al.*, 2010) and were deliberately chosen to span a range of possible ice conditions over the 21st century. Emissions in RCP 4.5 peak around 2040 and subsequently decline, representing a “stabilization”, while in RCP 8.5 emissions continue to increase over time at the current rate. This collection of climate scenarios and GCMs is designed to span the structural uncertainty of the geophysical models and the uncertainty of future human behaviour. Note that all of these global models are free-running realizations of large-scale conditions, unconstrained by data. As such they will not capture the details of any particular year (and in particular, the observed interannual and spatial details of 2006–2017); nonetheless, they should capture the present observed statistics of interannual variability, the expected changes in climate and variability over multiple decades, and the dominant spatial patterns observed in the real system (Hermann *et al.*, 2019). The years available to predict fish distribution were 2006–2099 except for CESM RCP 4.5, which was only available from 2006 to 2080; the “spin-up” year (2006) was removed from the analysis. Bottom temperature projections were corrected for overall bias and spatial bias by comparing the present day projections to observations from 2007 to 2017 recorded during EBS bottom trawl surveys (see [Supplementary Material S1](#) for details on bias correction). No observations of current speeds were available for bias correction, so the direct model output values from the multi-decadal simulations for these variables were used in the prediction.

Predictions of fish distributions using the Bering10K model predictions were averaged for four time periods: (i) present-day, 2013–2017, (ii) early mid-century, 2030–2039, (iii) late mid-century, 2060–2069, and (iv) end of century, 2090–2099. For each of the time periods, there were six realizations of the predicted variables (bottom temperature and bottom current speed) arising from the six climate projections. The best-fitting GAM for each species was used to predict the CPUE of the species for the EBS

on the 1 km² grid for each year. The significant variables in the best-fitting model were used to make predictions, including the significant static variables (depth, slope, sediment size, tidal current speed) and the temporally changing variables (bottom current speed and bottom temperature). For each time period, the spatially and temporally explicit predictions of CPUE for the species were made for individual years and then averaged across years, creating a single average distribution for the species for each time period for each of the six climate projections.

The first time period (present day, 2013–2017) was used to test the ability of the GAMs with Bering10K model output data to predict future distributions of fish species. The (2013–2017) predicted CPUE of each species was compared to observations at each of the 2013–2017 bottom trawl survey locations. Three measures were used to evaluate the use of GAM and Bering10K model predictions to predict future distributions: the deviance explained by a generalized linear model of observations against predictions (and the models statistical significance), the root mean squared error of the observations and predictions, and the model efficiency (Stow *et al.*, 2009; Olsen *et al.*, 2016) that measures how well the model predicts the observations relative to the average. The deviance explained, root mean squared error, and modelling efficiency were calculated for each of the six climate projections.

Predictions for the later time periods (early mid-century 2030–2039, late mid-century 2060–2069, and end of the century 2090–2099) were made for each species on 1 km² raster surfaces. These data were back-transformed to the original CPUE scale of the data for those groups that were log-transformed and areas with CPUE > 1 kg ha⁻¹ were considered as occupied by each species. Spatial analyses were then carried out on the raster surfaces for each species to determine the centre of gravity of the predicted CPUE and how this was predicted to change over time. Indices of aggregation and proportion of the EBS occupied (and their associated variances) were also computed using the SDMTTools package in R (VanDerWal *et al.*, 2019) for each species and model to evaluate the predicted expansion or contraction of over time. Finally, we calculated the proportion of each species surveyed abundance (the sum of the predicted CPUE in the area) that was predicted to move in or out of the standard EBS shelf bottom trawl survey area and into or out of the northern Bering Sea bottom trawl survey area. We tested for statistically significant differences in the trends (slopes) of changes in the centre of gravity, area occupied and proportion of the predicted CPUE inside the standard bottom trawl survey area for each species group using the analysis of covariance with year, climate model, and a climate model × year interaction term as explanatory variables. Significance was determined at the $p < 0.05$ level.

Results

The best-fitting GAMs developed for the EBS fish and crab species included all variables as significant, except in some cases the slope variable ([Supplementary Material S2](#)). The slope variable was not retaining in the best-fitting GAM for some flatfish [juvenile arrowtooth flounder (*Atheresthes stomias*), juvenile flathead sole (*Hippoglossoides elassodon*), yellowfin sole] and tanner crab. The models had depth as the most important variable, with the single exception being red king crab (*Paralithodes camtschaticus*) where tidal current was the most important variable in the modelling. Best-fitting models explained between 20 and 72% of the deviance in historical survey catches of groundfish and crab

from 1982 to 2012. The deviance explained for training data (1982–2012) was higher than the deviance explained for the testing data (2013–2017) across all species. On average there was ~46% drop in deviance explained when moving from the training data (average D^2 across all species = 0.47) to the testing data (average D^2 across all species from 0.26). However, the root-mean-squared-error and the model efficiencies indicated that the model performance on the testing data was much better than predictions based on the average CPUE. The only potential exceptions to these results was for juvenile and adult walleye pollock (*Gadus chalcogramma*) and red king crab where the best-fitting models explained 23, 29, and 60% of the deviance, respectively, but only 6% or less of the variability in the 2013–2017 present day output.

The relationships between CPUE and habitat variables followed similar patterns for certain groups of species (Supplementary Material S2). For example, the relationships between CPUE and sediment size, tidal current, and current speed were similar for flathead sole, arrowtooth flounder, and Alaska plaice (*Pleuronectes quadrituberculatus*), but depth and temperature show a different pattern for Alaska plaice than the other species. These relationships resulted in distinct patterns of distribution across the EBS (e.g. Figure 2 for Pacific cod and maps of distributions of additional species found in Supplementary Material S2).

Pacific cod (*Gadus macrocephalus*) were distributed mainly along the outer shelf of the EBS through much of the historical data, were abundant in the southwestern shelf, and moved towards the middle-inner shelf during 2002–2006 that includes warm years (Figure 2). This pattern was also predicted using the present day climate projections (2013–2017), a similarly warm period. The predictions under different climate models were similar within each radiative flux perturbation (RFP), even in the later decades (Figure 2), with the bulk of the predicted CPUE of cod still occurring on the outer shelf. However, under RFP 8.5, all projections show high CPUE areas moving north along the outer shelf and in general CPUE was predicted to increase across the middle-inner shelf as well (Figure 3). The predicted average distributions for other species generally followed these same patterns, with shifts in the overall distribution of CPUE within the southern EBS shelf but not distinct patterns of full immigration into new regions or emigration completely out of others. The shifts for most species are subtle, mostly demarcated by changes in high and low CPUE areas (Supplementary Material S2). This is partly due to the direction of the shifts changing between time periods, as can be seen in Pacific cod, which show an initial shift inshore, towards the inner domain, but by the end of the century and under the warmer RCP 8.5, they shift back to the middle domain.

Evidence for subtle shifts in distribution can also be found in the changes in weighted centre of gravity for each of the groundfish and invertebrate groups from the early years (1982–2012) to the late century (Figure 4). With the exception of juvenile Pacific cod, the mean movement of all taxonomic groups was predicted to be <75 km in any direction from historical patterns to late century predictions. The centre of gravity for the distribution of juvenile Pacific cod was predicted to move 202 km from the historical centre of gravity. Figure 4 shows that in most cases the shift from early years (1982–2012) to late century (2090–2099) was to the north: arrowtooth flounder (juveniles = 14 km, adults = 36 km), flathead sole (juveniles = 16 km, adults = 6 km),

northern rock sole (juveniles = 12 km, adults = 13 km), yellowfin sole (*Limanda aspera*) (juveniles = 1 km, adults = 6 km), walleye pollock (juveniles = 47 km, adults = 39 km), and tanner crab (7 km). Notable are the two species where the centre of distribution shifts southwards: Alaska plaice (73 km) and snow crab (40 km). The slope of these trends in northward or southward distribution was all statistically significant ($p < 0.05$). Only Pacific cod (adults and juveniles) and red king crab did not show significant trends in north–south movement over time. Another notable result was the significance of the interaction term between climate model and year for all species groups except juvenile yellowfin sole ($p = 0.22$), indicating that the different climate models often had different trends in north–south distribution shifts. For example, the slope of the trend in northward shift for tanner crab was significantly higher for the CESM 8.5, MIROC 8.5, and GFDL 8.5 climate scenarios than for the corresponding 4.5 scenarios (Figure 4). Unsurprisingly, this was a consistent pattern across species that showed significant northward shifts.

The patterns in cross-shelf (east–west) distribution shifts were mixed (Figure 5). In total, five species groups showed significant ($p < 0.05$) trends in eastward movement of the centre of gravity of their distribution (Alaska plaice = 18 km, juvenile and adult flathead sole = 11 and 4 km respectively, juvenile Pacific cod = 201 km and tanner crab = 9 km), while five showed significant westward movement (juvenile and adult northern rock sole = 7 and 5 km respectively, adult yellowfin sole = 8 km, juvenile walleye pollock = 6 km, and snow crab = 9 km), and the rest of the groups showed no significant trend in cross-shelf movement (Figure 5). As with northward movement, there were significant year \times climate model interactions for all but four species groups (Alaska plaice, juvenile flathead sole, and juvenile and adult yellowfin sole) indicating that the different climate scenarios had different slope for east–west distribution trends. Again, the 8.5 scenarios tended to produce steeper slopes for change in east–west distribution than the 4.5 climate scenarios (Figure 5).

The proportion of the EBS occupied (area occupied) increased significantly for 12 of the 16 species groups (Figure 6). The largest increases in predicted area occupied were for juvenile and adult flathead sole and arrowtooth flounder. Significant decreasing trends in area occupied were predicted for Alaska plaice and snow crab, while adult northern rock sole and tanner crab did not have significant trends over time. Except for red king crab, all of these changes in area occupied were positively correlated to changes in abundance (measured by the sum of the predicted CPUE). This would imply that, for most species, the change in distribution is related to a change in overall abundance, rather than a change in distribution caused by environmental changes. As with the predictions of the centre of gravity, the climate scenarios with larger predicted warming (CESM 8.5, MIROC 8.5 and GFDL 8.5) tended to produce the strongest response in terms of area occupied by the species groups (Figure 6).

Finally, the models predict that there will be changes in the distribution of groundfish and crabs relative to the current bottom trawl survey areas. In all species groups except tanner crab, there was a significant trend in the proportion of the CPUE predicted to be within the standard bottom trawl survey area (Figure 7). For 12 of the species groups examined, shifts of biomass out of the standard survey area were predicted, ranging from small shifts of <1% such as for adult flathead sole to larger shifts of ~10% for juvenile walleye pollock (Figure 7). Three species show trends of significant increases in the proportion of the biomass currently

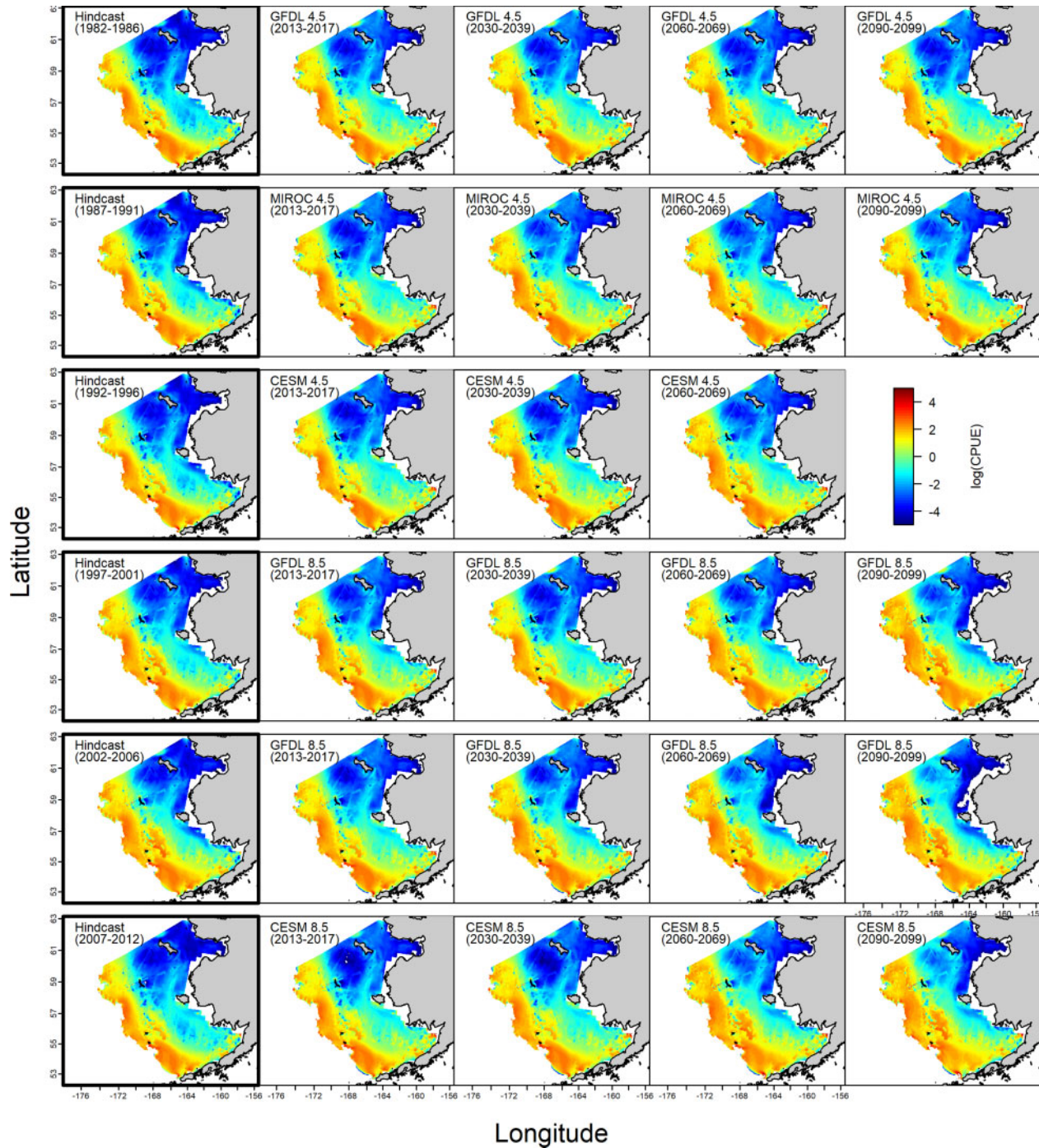


Figure 2. Predicted distributions of Pacific cod in past years (far left, graphs outlined in heavier borders), and four future periods: (left to right, second to fifth column): current, early mid-century, late mid-century, and end of century, using six climate projections: three GCMs, RFP 4.5 (top), 8.5 (bottom).

inside the bottom trawl survey area (snow crab, juvenile Pacific cod, and Alaska plaice). On average none of the overall effects were >10%, but the variance in predicted distribution for especially the late century years was high. For example, between 10 and 25% of the juvenile walleye pollock would be expected to be found outside the standard survey area within the northern Bering Sea by the late century depending on the climate scenario (Figure 7). As with the previous analyses of centre of gravity and

area occupied, there were significantly different trends among models, with the 8.5 climate models showing greater effects over time on the distribution of the species groups.

Discussion

Projections under all climate scenarios predicted similar patterns in future years, with trends more pronounced under increasingly higher emissions at the end of the century—RFP 8.5. The thermal

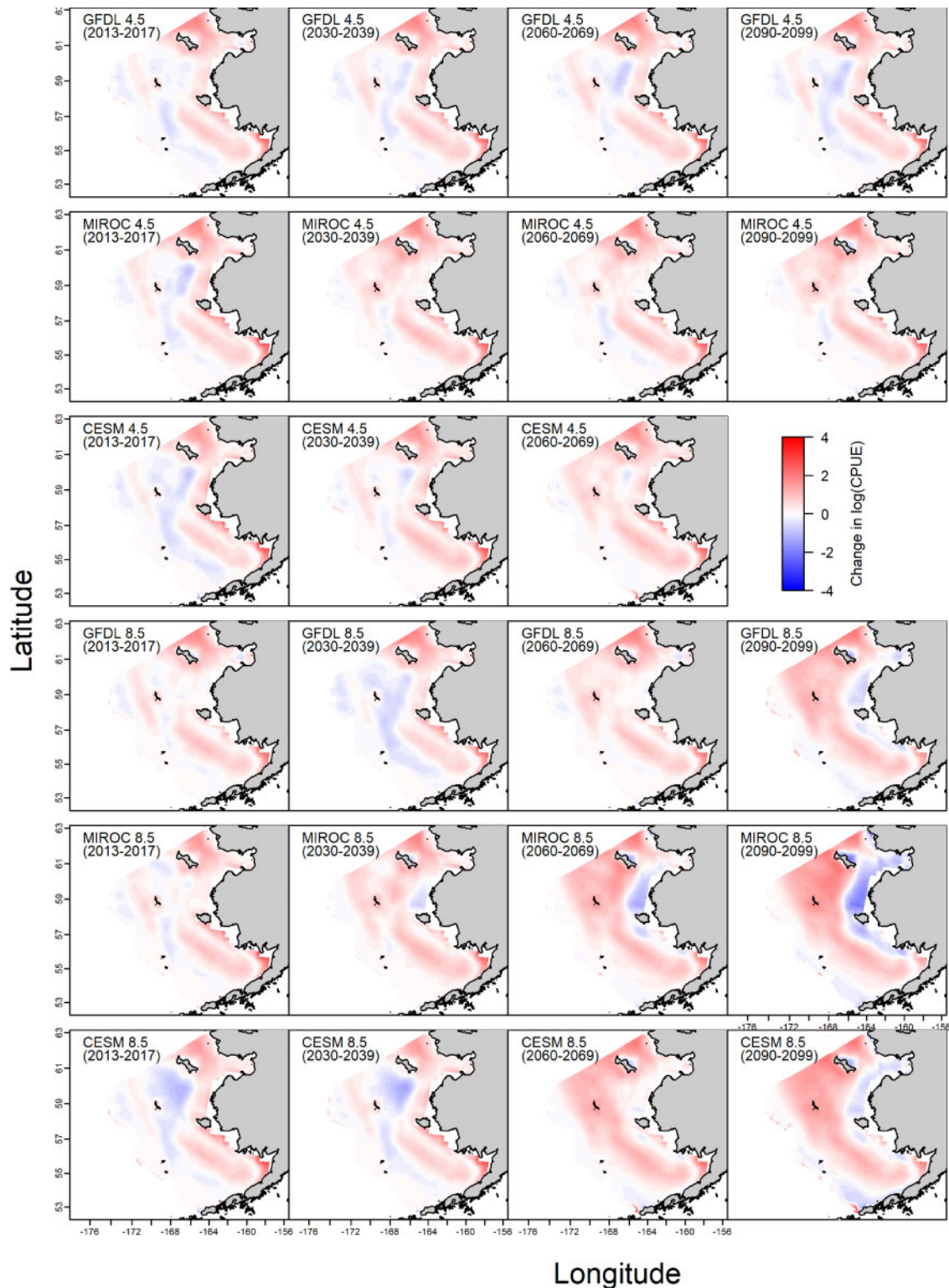


Figure 3. Predicted change in distribution of CPUE of Pacific cod relative to the average from 1982 to 2006. Current, early mid-century, late mid-century, and end of century, using six climate projections: three GCMs, RFP 4.5 (top), 8.5 (bottom).

envelope in the projections is coolest for GFDL 4.5 and warmest for MIROC 8.5. Given the recent heatwaves and lack of sea-ice across the Bering Sea shelf, which were not expected until mid-century, it is RFP 8.5 that seems more likely to predict future

environmental conditions and hence fish distributions. The projected increase in temperature from the current period to the end of the century was 1.22°C averaged across all models (including the shelf, slope, and northern Bering Sea), ranging from -0.15°C

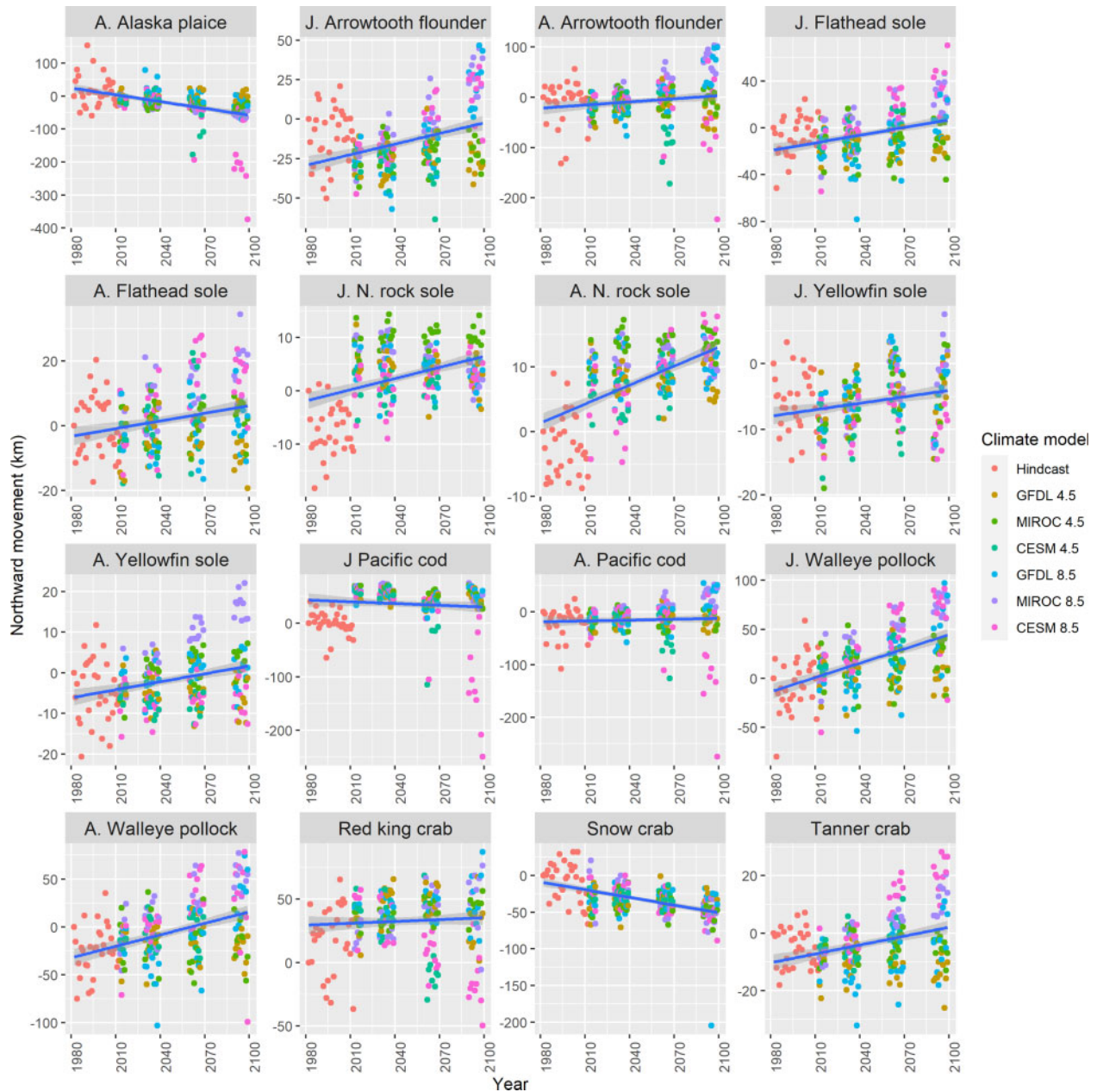


Figure 4. Northward shift of the centre of gravity for sixteen groups of groundfish species in the eastern Bering Sea predicted under six climate projections. Abbreviations are A = adult, J = juvenile, and N = northern. The line indicates the average trend in the centre of gravity across all models.

(GFDL 4.5) to 2.12°C (CESM 8.5). For about half of the groups (adult Pacific cod, arrowtooth flounder, flathead sole, and walleye pollock), the modelling indicated that depth and bottom temperature were the most important significant variables (indicated by the approximate *F*-statistic in the GAM) determining species distribution. Bottom temperature was a significant variable in all models. This is consistent with other studies of the historical bottom trawl survey and temperature data from the EBS (e.g. Mueter and Litzow, 2008; Thorson, 2019). It is also consistent with other EBS studies that have linked species habitat preferences to prey preferences and prey abundance (McConnaughey and Smith, 2000; Yeung and Yang, 2014), sediment types

(Rooper *et al.*, 2005), and depth (Laman *et al.*, 2018). With the exception of Pacific cod and walleye pollock, all the species examined here (flatfish and crab) are benthic. Pacific cod and walleye pollock could potentially migrate vertically to maintain a preferred temperature while maintaining the same geographical position. However, both cod and walleye pollock showed declining CPUE at temperatures above 6°C and the regional ocean models generally show that future warming is greater in the upper water column than near the seafloor (Hermann *et al.*, 2016), indicating that vertical movement is likely not an option for even the least benthic of the species to avoid the effects of warming.

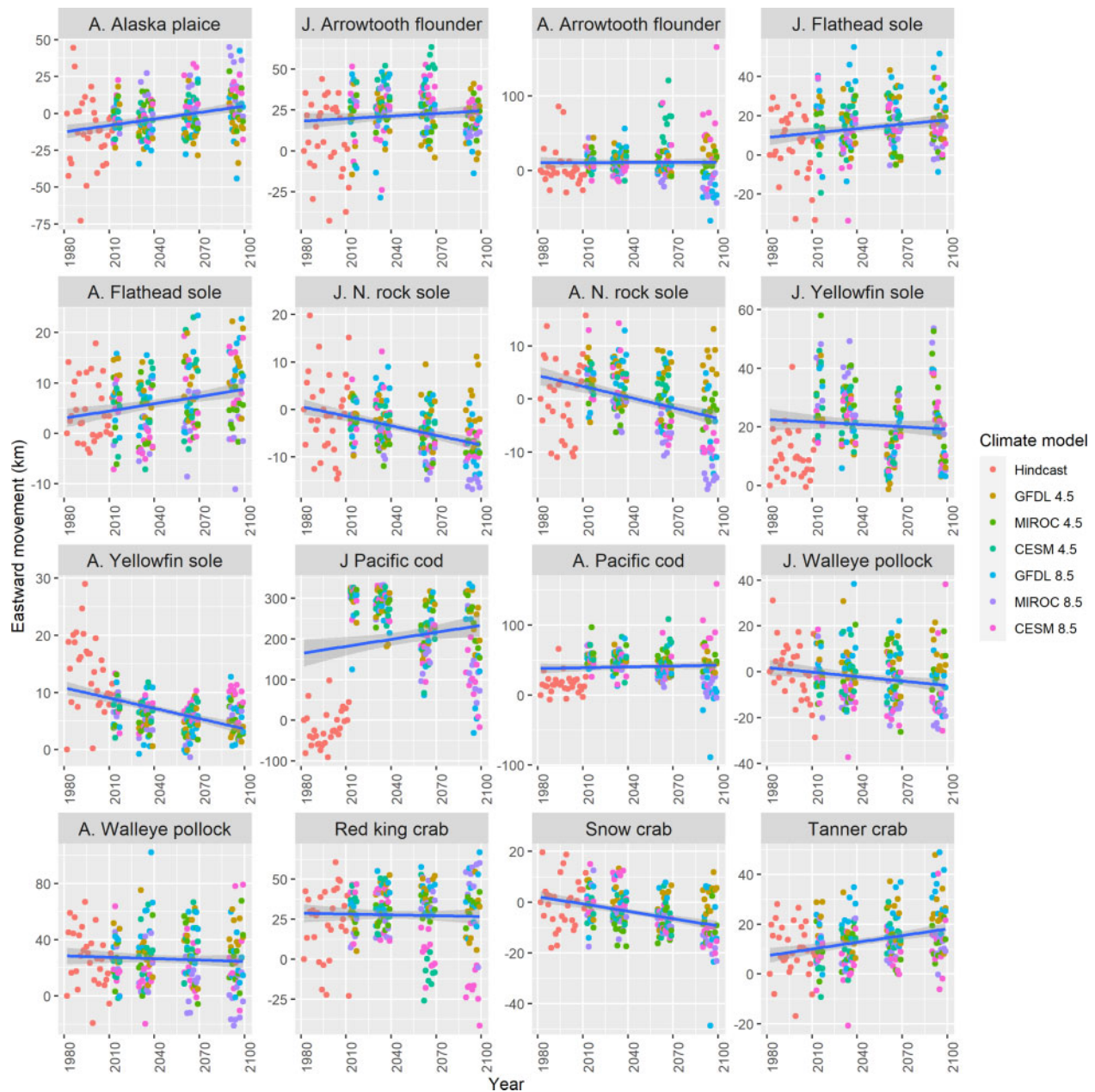


Figure 5. Eastward shift of the centre of gravity for sixteen groups of groundfish species in the eastern Bering Sea predicted under six climate projections. Abbreviations are A = adult, J = juvenile, and N = northern. The line indicates the average trend in the centre of gravity across all models.

Previous analyses of distribution shifts in the EBS suggest that historical (1982–2006) shifts in groundfish centre of distribution averaged 34 km (SD = 56 km) and that for most species the historical shift was not statistically significant ($\sim 65\%$ of the species examined; Mueter and Litzow, 2008). The increase in bottom temperature from 1982 to 2006 was $\sim 1\text{--}1.5^\circ\text{C}$ (Mueter and Litzow, 2008). This is consistent with our analysis of an overlapping set of 16 groups of groundfish and crab where predicted shifts in the centre of gravity averaged 35.2 km (SD = 48.1 km) from the historical time period (1982–2012) to the end of the century (2090–2099) with a corresponding 1.22°C temperature increase (averaged across models) from the present day to the

end of the century. Our analyses did show that these trends were statistically significant. In other ecosystems such as the US west coast and the Gulf of Alaska, the influence of climate change has been predicted to be larger (Pinsky *et al.*, 2013; Morley *et al.*, 2018). However, observational data such as analyses by Mueter and Litzow (2008) and Dulvy *et al.* (2008) showed historical changes in distribution of <60 km, with some mitigation of latitudinal changes by movement towards deeper cooler waters.

The results of this modelling also indicate that some of the shifts in distribution were due to changing abundance (e.g. adult walleye pollock was predicted to increase in abundance overall and expand their area occupied to the north), or to actual shifts

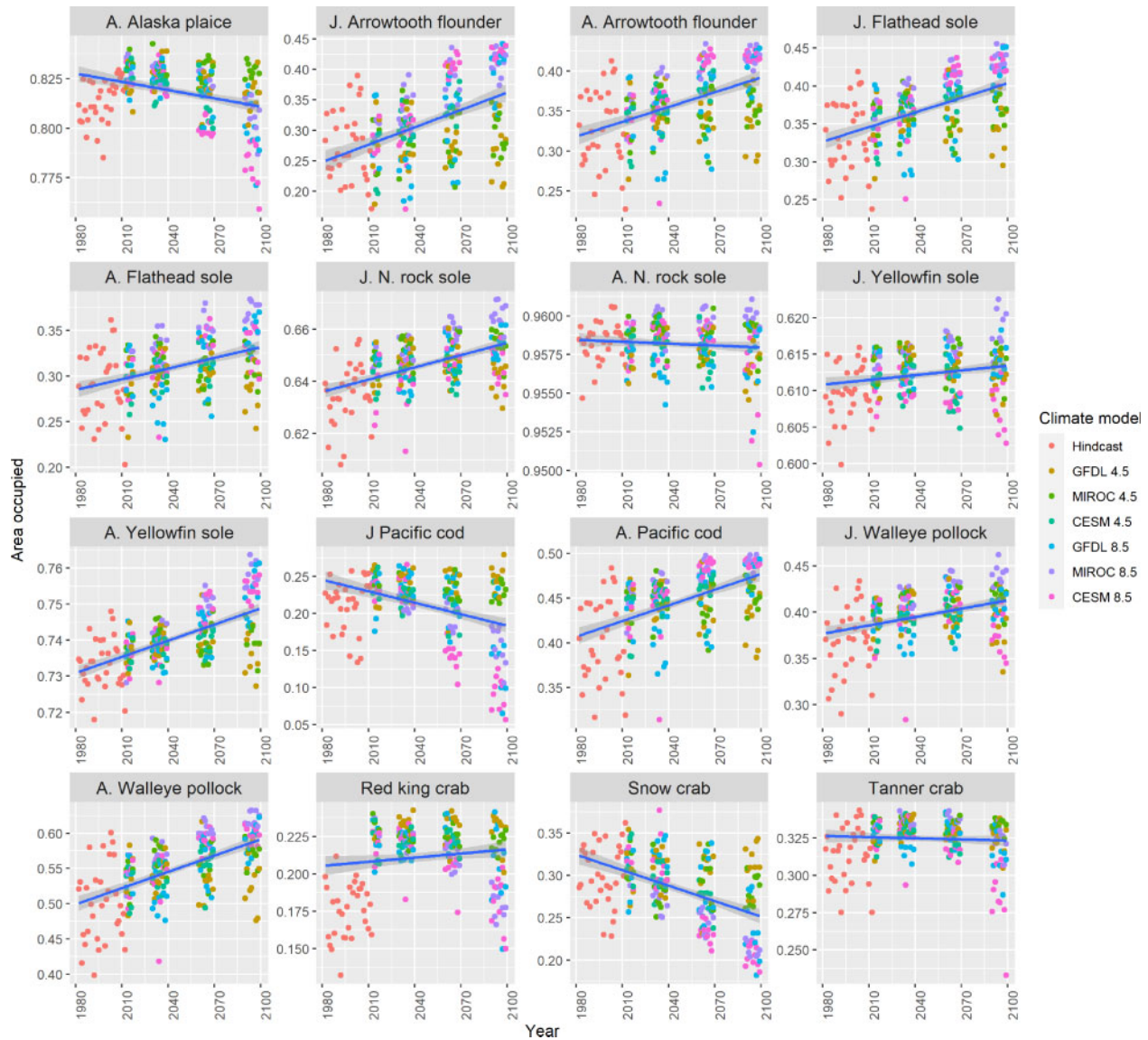


Figure 6. Proportion of the combined eastern Bering Sea and Northern Bering Sea occupied (at densities $>1 \text{ kg ha}^{-1}$) for 16 groundfish species (or species life history stages) predicted under six climate projections. The line represents the overall time trend. Abbreviations are A = adult, J = juvenile, and N = northern.

in the distribution (e.g. the abundance and area occupied by tanner crab although correlated were expected to stay relatively constant over time, while their distribution shifted north and east). Adult Pacific cod showed virtually no movement in their centre of gravity, yet their area occupied and abundance were predicted to increase in the EBS, indicating a potentially even distribution of the increased abundance between new and already occupied areas. While the future decrease or lack of sea ice and areas with temperatures below zero ($<0^{\circ}\text{C}$) seem to open large areas to some species such as Pacific cod, it is unknown what the long-term effect will be on phytoplankton and cold water zooplankton species at the base of their food web. Thus, the predicted shifts in distribution models were complex and variable among species, indicating that a non-uniform community reorganization is likely to occur with warming temperature in the EBS.

The modelling study presented here is limited to only future temperature and current effects. This approach did not address potential changes in food web dynamics across the EBS, which has been suggested as a major force structuring distributions of fishes. Evidence from prior studies in EBS indicates that the timing of phytoplankton blooms is likely to be earlier and the zooplankton abundance is likely to be lower in warmer temperatures, with cascading effects up the food chain to fishes (Sigler *et al.*, 2014, 2016). In addition, food limitation for gadoids (walleye pollock and Pacific cod) has been shown to affect their distributions in previous studies. For example, pollock size classes have been observed in acoustic and trawl surveys to move in response to food availability (Kotwicki *et al.*, 2005) and changes in pollock distribution and abundance have been linked to overlap with prey resources (Boldt *et al.*, 2012) and abundance (Mueter *et al.*, 2006; Hunt *et al.*, 2011). Predatory fishes, such as arrowtooth

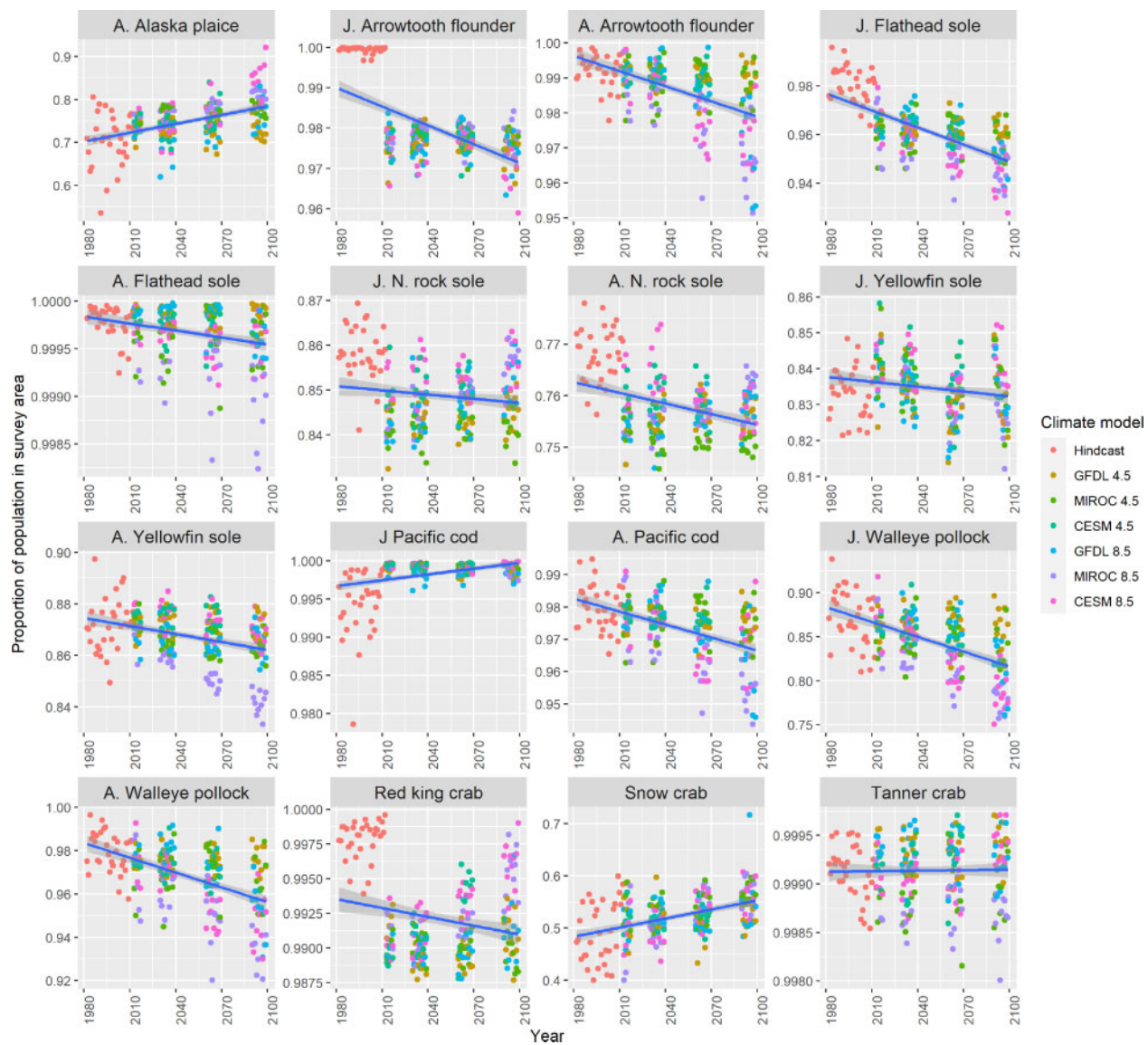


Figure 7. Proportion of abundance predicted to be inside the standard eastern Bering Sea bottom trawl survey area for 16 groundfish species (or species life history stages) under projections of six climate scenarios. The line represents the overall time trend. Abbreviations are A = adult, J = juvenile, and N = northern.

flounder, may also change their distribution in response to prey resources, such as juvenile walleye pollock (Ciannelli *et al.*, 2012). In addition, some other variables such as extent of winter ice cover were missing from our analyses. The influence of the extent of sea ice in the EBS and the resulting cold pool on bottom temperatures has been well documented (Stabeno *et al.*, 2001; Stabeno *et al.*, 2010; Stabeno *et al.*, 2012), along with the influence of the cold pool on biota distributions and interactions (Mueter and Litzow, 2008; Boldt *et al.*, 2012; Nichol *et al.*, 2019). As the Bering10K model does not predict the extent of ice coverage over the eastern Bering Sea, it was not possible to include this variable that is known to be important to fish distribution. These gaps in explanatory variables point out the weaknesses in the models and also create uncertainty in the predictions of future fish distributions; they possibly account for some of the unresolved spatial patterns in the model residuals.

The distributional changes predicted for groundfish by this study were modest, but the ecological implications of these changes could be important. In part, the modest distributional change reflects the modest differences in bottom temperature predicted by the different Bering10K climate projections. The temperature change was 1.22°C from the present-day projections (2013–2017) to the late century (2090–2099). However, observed and modelled temperature variations can be much higher from year to year. For example, the difference in observed temperature measured at standard bottom trawl survey stations in the EBS from 2013 to 2014 was 1.38°C and, from 2016 to 2017 the difference was –1.26°C. For mobile fish, the ability to redistribute and avoid relatively short-term events of suboptimal conditions has been linked to changes in distribution (Kotwicki *et al.*, 2005; Stevenson and Lauth, 2019) and even perceived abundance (Nichol *et al.*, 2019). In particular, 27% of the Pacific cod biomass

in the bottom trawl surveys of 2017 and 2019 was found to occur in the northern Bering Sea (Thompson and Thorson, 2019). This is in sharp contrast to the <1% of the cod biomass that was found in the northern Bering Sea during the 2010 survey. In 2010, the northern Bering Sea waters were generally <2°C except in the shallowest nearshore areas, while in 2017 and 2019 waters >2°C were found across most of the northern Bering Sea (Stevenson and Lauth, 2019). This may have allowed Pacific cod to redistribute into the northern Bering Sea as indicated by the large increase in biomass. The Bering10K model predictions showed these types of increases in bottom temperature for the northern Bering Sea only in the late-century projections under the RCP 8.5 scenarios. This may in part explain the differences between the observed shifts in distribution and the predictions from the model; however, looking at the late-century predictions for adult cod, the proportion of the abundance predicted to be outside the survey area (in the northern Bering Sea) was only 4–6% (Figure 7). This may point again to other factors besides just the effect of avoiding unsuitable temperature on the distribution of fish. For example, the recent marine heatwave in the Gulf of Alaska reduced the forage base and body condition of Pacific cod potentially leading to increased mortality (A'mar and Palsson, 2015; Barbeaux *et al.*, 2017) and the distribution of commercial fishing for Pacific cod in the EBS was still concentrated inside the standard survey area in 2017 and 2019 (Thompson and Thorson, 2019). Spatial patterns of increases in mortality due to temperature-based mechanisms or fishing mortality patterns, such as these were not directly accounted for in our analyses of CPUE, but could also explain some of the discrepancies between observed and predicted distributions. These studies have shown that there have been recent large-scale shifts in the distribution of species into the northern Bering Sea in response to large temperature changes that were not captured in the Bering10K model predictions.

Although the long-term average shift in distribution for groundfish in the EBS is less striking than the year-to-year shifts, the implications of this study are important as they reflect the long-term mean shifts in groundfish populations and provide a basis for understanding which populations might expand and contract in future years and what are the timelines in which these shifts may be observed. This has important ramifications for monitoring activities such as fisheries independent surveys since additional areas may need to be added to the standard survey to account for species movement in and out of this fixed survey area. The analyses and modelling presented here provide an indication that current management and survey schemes may have to undergo changes in future years to account for changes in species distributions (Ianelli *et al.*, 2011; Haynie and Pfeiffer, 2013). Although our study does not allow estimates of biomass of shifts outside the Exclusive Economic Zone, some species distributions extend to the very edge of US territorial waters with high CPUE; thus, movement out of US jurisdiction is likely. Similarly, although the centre of gravity may shift only slightly as shown here, EFH maps for the EBS may need to be revised further, if distribution shifts to previously scarcely occupied areas become more consistent. The modelling presented here would indicate that on average the area defined as EFH (currently the upper 95% of cumulative CPUE) for a species is likely to change. For example, the area occupied by adult arrowtooth flounder is predicted to increase by up to 20% by the late-century relative to the current distribution, while the centre of gravity of the distribution moves

~18 km NE, necessitating a change to the current definition of EFH. Studying the potential distributional shifts in groundfish in response to climate change should allow for appropriate management actions to anticipate effects on fish populations and account in advance for the effects of warming temperatures on ecosystems.

Supplementary data

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

Data availability statement

The bottom trawl survey data used in these analyses are available from the AKFIN data base at <https://akfin.psmfc.org>. Bathymetry and environmental variable data and R code underlying this article will be shared on reasonable request to the corresponding author.

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