

## Locational Shifts in the Summer Flounder Fishery: Overview for MAFMC Meeting

### Context:

Our research describes movements in fishing activity for federal commercial fisheries in the Mid-Atlantic and Northeast regions. Using data compiled from vessel trip reports, we calculated average annual locations of fishing activity and aggregated this data by port, species, gear types and vessel size. In this presentation, we focus on locational shifts in fishing activity for summer flounder to inform those participating in the FMP revision for this species.

### Presentation Overview:

Movement in summer flounder biomass has emerged as a concern in management of the fishery. The degree to which fishing activity patterns have mirrored these changes was until now largely unknown, limiting understanding of linkages between ecological and social change. Rapid locational shifts in fishing activity pose several challenges for U.S. fisheries management, that like many management systems relies on the allocation of resource access among static, spatial governance units (e.g. states, regions). This presentation addresses this gap by describing shifts in fishing activity in the commercial summer flounder fishery from 1996-2014.

We use a mixed-methods approach to describe this locational shift and interpret potential considerations for the policy process. First, vessel trip report data is used to track shifts in the average annual location of fishing activity for summer flounder in the New England and Mid-Atlantic management regions. Locational shift in the fishery is broken down by state, to allow for nuanced consideration of how shifts impact different groups of resource users. Second, we assessed written and verbal public comments during the scoping period for the FMP revision to contextualize the spatial patterns that appear in the data. The movement described in the spatial analysis corresponds with the emergence of two main narratives for management change, “quota re-allocation” and “landings flexibility.”

### Support:

This project is funded by the National Socio-Environmental Synthesis Center Graduate Pursuit Program, and supported through collaboration with Drs. Malin Pinsky and Kevin St. Martin of Rutgers University (NSF Coastal SEES Award # 1426891).



## 31 **Abstract**

32 Recent shifts in the geographic distribution of marine species have been linked to shifts in  
33 preferred thermal habitats. These shifts in distribution have already posed challenges for living  
34 marine resource management, and there is a strong need for projections of how species might be  
35 impacted by future changes in ocean temperatures during the 21<sup>st</sup> century. We modeled thermal  
36 habitat for 686 marine species in the Atlantic and Pacific oceans using long-term ecological  
37 survey data from the North American continental shelves. These habitat models were coupled to  
38 output from sixteen general circulation models that were run under high (RCP 8.5) and low (RCP  
39 2.6) future greenhouse gas emission scenarios over the 21<sup>st</sup> century to produce 32 possible future  
40 outcomes for each species. The models generally agreed on the magnitude and direction of future  
41 shifts for some species (448 or 429 under RCP8.5 and RCP2.6, respectively), but strongly  
42 disagreed for other species (116 or 120 respectively). This allowed us to identify species with  
43 more or less robust predictions. Future shifts in species distributions were generally poleward  
44 and followed the coastline, but also varied among regions and species. Species from the U.S. and  
45 Canadian west coast including the Gulf of Alaska had the highest projected magnitude shifts in  
46 distribution, and many species shifted more than 1000 km under the high greenhouse gas  
47 emissions scenario. Following a strong mitigation scenario consistent with the Paris Agreement  
48 would likely produce substantially smaller shifts and less disruption to marine management  
49 efforts. Our projections offer an important tool for identifying species, fisheries, and  
50 management efforts that are particularly vulnerable to climate change impacts.

51

52

## 53 **Introduction**

54           A major impact of climate change in the oceans has been the redistribution of marine  
55 organisms, which have generally been shifting poleward or into deeper waters as temperatures  
56 warm [1, 2]. Long-term shifts in species distributions have been linked to directional shifts in  
57 their preferred temperatures [3, 4], as the geographic distributions of marine species are strongly  
58 linked to temperature tolerance [1]. Further, regional species productivity [5, 6] and phenology  
59 [7, 8] can be highly sensitive to variation in water temperatures, which may be a driver of long-  
60 term shifts [9]. The implications of geographic shifts of marine species have already been  
61 observed in global fisheries catches and changes in catch composition from regional landings  
62 data are consistent with poleward shifts in species distributions [10].

63           The North American continental shelf is an expansive area with some of the most  
64 productive fisheries globally [11]. This diverse area also contains some of the most rapidly  
65 increasing regions of ocean temperature in the world [12, 13]. The rising temperatures have been  
66 linked to major shifts in the distribution of some species [3, 14]. These shifts have led to  
67 conflicts between regions over fisheries catch allocation as species shift across management  
68 boundaries [15, 16]. Global ocean temperatures are projected to continue rising [17] and areas of  
69 the Northeast American shelf may experience some of the most extreme increases [18].  
70 Associated with this warming are predictions for substantial shifts in regional fisheries  
71 productivity [11]. Predictions for how ocean warming will impact the living marine resources of  
72 the United States and Canada are currently a priority for federal management [19–21].

73           Projections of future species distribution shifts and biomass changes are an emerging tool  
74 for anticipating climate change impacts on marine systems. Predictions about how species will  
75 respond to ocean warming are often made by coupling models of species thermal habitat with

76 output from climate projection models [22]. Generally, species projection studies indicate that  
77 biomass will shift with preferred thermal habitat [23–25], but shifts may be constrained by other  
78 habitat features such as depth [26], seafloor complexity [27], or primary productivity [28].  
79 Further, for some species, annual temperature extremes instead of thermal averages can be a  
80 primary driver of projected shifts in distribution [29, 30] or of regional biomass [31].

81       Previous studies that projected species distribution changes have been limited for two  
82 major reasons. First, the spatial extents for species distribution projections are often restricted to  
83 regional scales [24, 26, 27]. While these regional perspectives are valuable, they limit our ability  
84 to anticipate the larger scale changes that will occur over the entire range of species. Further,  
85 species habitat models are often based on data from only a portion of the total geographic range,  
86 and thus may fail to capture the full extent of a species' realized thermal niche. For instance,  
87 climate change may introduce novel conditions to a region, such as higher annual maximum  
88 temperatures, which may be unrepresented in habitat models built from narrow-scale data. In  
89 contrast, some notable species projection efforts have been global in scope [25, 32], but these  
90 have often been at a coarse spatial grain that makes it more challenging to define accurate  
91 thermal envelopes for marine species. The coarse spatial grain of these latter studies also makes  
92 them less directly useful at the regional scales that are particularly relevant for questions of  
93 community turnover and resource management. A second limitation of many previous studies  
94 has been a relative lack of uncertainty estimates for predictions among species [33, 34].  
95 Uncertainty in projections of species distribution comes from multiple sources, including  
96 uncertainty over future greenhouse gas emissions scenarios, variation among climate projection  
97 model predictions, natural internal variability inherent in the climate system, structural  
98 differences among species distribution models, and parameter uncertainty in species distribution

99 models. The first three factors impact predictions of regional ocean temperature changes [35] and  
100 can lead to a wide range of predicted outcomes for individual species [29, 31, 36]. There have  
101 been relatively few marine species distribution projections to date, and it remains unclear how  
102 much uncertainty is acceptable for a projection to be useful. Conducting projections on multiple  
103 species within a standard format for assessing uncertainty can provide opportunities for  
104 identifying species with more or less robust predictions [23, 28].

105         Here we summarize results from a comprehensive effort to project future distributions of  
106 686 marine species on the North American continental shelf. For each species, we generated  
107 predictions of their distribution throughout the 21<sup>st</sup> century using sixteen fully coupled general  
108 circulation models, each run under a low (Representative Concentration Pathway (RCP) 2.6) and  
109 high (RCP8.5) future greenhouse gas emission scenario. Thus, thirty-two projections were  
110 simulated for each species. We used three metrics for identifying species with more uncertain or  
111 more robust projections based on agreement among modeled outcomes. We have expanded on  
112 previous efforts to predict the responses of marine species to climate change by combining  
113 extensive survey data from around the continent in order to better define each species' thermal  
114 habitat. Finally, we projected distribution shifts for each species across the North American shelf  
115 in order to include a large portion of species' distributions, rather than limiting the predictions to  
116 individual oceanic basins. Compared to previous studies, our projections suggest some of the  
117 largest future shifts in species distribution, many exceeding 1000 km. We found that the  
118 geometry of the continental shelf played an important role in determining whether species were  
119 projected to shift more or less over the 21<sup>st</sup> century.

120

121

## 122 METHODS

### 123 Survey data

124 Species occurrence and biomass data were taken from 136,044 bottom trawl hauls from  
125 twenty long-term surveys that encompassed a majority of the continental shelf regions around  
126 the United States and Canada (Fig 1). Within six of the sampling regions, separate surveys were  
127 conducted in multiple seasons (Table 1). Most of the survey data have been used in previous  
128 studies [3, 9, 37, 38]. A majority of the data from the United States were obtained from the  
129 *trawlData* package [37] used with R software version 3.3.2 [39].

130

131 **Fig 1. Biological survey regions.** Locations for 136,044 bottom trawl hauls from long-term  
132 ecological surveys conducted on the North American continental shelf. Hauls are colored to  
133 indicate the different survey regions described in Table 1.

134

135 **Table 1. Information for North American bottom trawl surveys.**

Region	Seasons	Years	# hauls	Color	Agency
Aleutian Islands	Summer	1983-2014	4588	Red	Alaska Fisheries Science Center, NOAA
Eastern Bering Sea	Summer	1982-2014	12210	Blue	Alaska Fisheries Science Center, NOAA
Gulf of Alaska	Summer	1984-2013	9578	Green	Alaska Fisheries Science Center, NOAA
West Coast Triennial	Summer	1977-2004	4544	Orange	Alaska Fisheries Science Center, NOAA
West Coast Annual	Summer	2003-2014	7589	Orange	Northwest Fisheries Science Center, NOAA
Gulf of Mexico (SEAMAP)	Summer	1982-2014	9277	Cyan	Gulf States Marine Fisheries Commission
Southeast U.S. Shelf (SEAMAP-SA)	Fall	1983-2014	9564		
	Spring	1990-2015	2614	Black	South Carolina Department of Natural Resources
	Summer	1989-2015	2384		
Northeast U.S. Shelf	Fall	1989-2015	2595		
	Spring	1968-2015	16472	Orange	Northeast Fisheries Science Center, NOAA
Northeast U.S. Inner Shelf (NEAMAP)	Fall	1963-2014	17767		
	Spring	2008-2015	1171	Red	Virginia Institute of Marine Science (VIMS)

Scotian Shelf	Fall	2007-2015	1307	Purple	Department of Fisheries and Oceans (DFO), Canada
	Spring	1979-2011	5217		
Southern Gulf of St. Lawrence Newfoundland and Labrador	Summer	1970-2011	7517	Green	Department of Fisheries and Oceans (DFO), Canada
	Fall	1978-1986	1114		
	Summer	1971-2009	5142	Blue	Department of Fisheries and Oceans (DFO), Canada
	Spring	1996-2011	4540		
	Fall	1995-2011	10854		

---

136

137 The season of biological sampling, years of survey data used, number of hauls, color indicator  
 138 for reference to Fig 1, and conducting agency for twenty regional bottom trawl surveys that were  
 139 used for fitting species thermal habitat models.

140

141

142 Within each survey, non-standard hauls were omitted (e.g., those with non-standard trawl

143 dimensions or mesh size) in order to ensure consistent sampling gear within surveys. Trawl catch

144 by species was expressed as biomass per unit area swept. Only species-level taxa were

145 considered for distribution modeling. Species names were standardized across surveys. When a

146 species was recorded separately by sex or maturity stage, these biomasses were summed before

147 further analysis. Egg and larval stage samples were excluded from analyses. Because surveys

148 comprehensively record the species found, survey records were expanded to include zeros

149 (observed absences) for species not observed in a given haul, but that were observed in other

150 surveys conducted on the same coast (i.e., Atlantic or Pacific). In addition, we added near-zero

151 biomass values ( $1.0^{-10}$ ) for a fraction of the hauls in regions where a species was never observed

152 (10% of the hauls in a region or 10% of total observations, whichever was smaller) in order to

153 facilitate fitting the full thermal envelope for species biomass models only (i.e., this does not

154 affect presence-absence models, see below). These near-zero values were important to allow

155 biomass models to include a larger range of environmental conditions—as opposed to being

156 restricted to a species present range—which was necessary to conduct biomass predictions at the

157 scale of the North American continental shelf. This approach is similar to the use of

158 “pseudoabsences” in distribution models that are based on presence-only data [e.g., 40], which  
159 are used to develop contrasts between suitable and unsuitable habitats.

## 160 **Environmental data**

161       Sea surface and bottom water temperatures for each haul were obtained from the Simple  
162 Ocean Data Assimilation (SODA3.3.1) reanalysis of ocean climate, which provides a global  
163 reconstruction of historical ocean temperatures [41]. SODA3.3.1 has a spatial resolution of 28  
164 km at the equator with increasingly finer resolution towards the poles ( $0.25^\circ$  latitude  $\times$   $0.25^\circ$   
165 longitude), and it has a 5-day temporal resolution beginning in 1980. For hauls occurring before  
166 1980, we used the SODA2.2.4 data, which has a  $0.5^\circ$  spatial resolution and monthly temporal  
167 resolution. For each haul, we recorded the seasonal average temperature by calculating the  
168 average surface and bottom temperatures for a three-month period (including the month when  
169 the haul took place and the preceding and following months) and by using the appropriate SODA  
170 grid cell based on haul location. This time-interval was chosen to match our projections, which  
171 were based on seasonal average temperatures in future years. To check that the SODA-derived  
172 seasonal surface and bottom temperatures were reasonable, we compared them to the surface and  
173 bottom water temperatures measured at each haul (i.e., not seasonal means) during the course of  
174 the surveys. The SODA-derived seasonal average temperatures that we used in the species  
175 habitat models were highly correlated with *in situ* measured temperatures (surface temperatures:  
176 slope(se) = 0.906(0.001),  $P < 0.001$ ,  $r^2 = 0.90$ ,  $DF = 102048$ ; bottom temperatures: slope(se) =  
177 1.003(0.001),  $P < 0.001$ ,  $r^2 = 0.86$ ,  $DF = 120859$ ).

178       Marine species temperature preferences are often modeled by only using observed  
179 temperatures that are recorded at the time of sampling [3, 24, 27]. However, annual temperature  
180 extremes including the summer maximum and winter minimum are also important factors

181 shaping the geographic distribution of marine species [1, 9, 42, 43]. Therefore, we also included  
182 the maximum surface and bottom temperatures and the minimum bottom temperature during the  
183 preceding twelve-month period for each haul, which were extracted from the SODA data set  
184 based on the date and location of each haul. Minimum surface temperature was excluded because  
185 it was highly correlated with minimum bottom temperature (slope(se) = 1.027(0.001),  $P < 0.001$ ,  
186  $r^2 = 0.87$ ,  $DF = 136126$ ).

187 The distribution of marine species on the continental shelf can also be influenced by  
188 seafloor rugosity (a measure of the spatial variation in depth) and sediment type [27, 44]. To  
189 calculate seafloor rugosity, we obtained depth data from the GEBCO gridded bathymetric data  
190 set for the North American shelf at  $\sim 1$  km resolution [45]. Rugosity was calculated as the mean  
191 of the absolute differences between a given grid cell depth and the depths of the eight  
192 surrounding cells using the *raster* package in R [46]. To reduce computation time, rugosity was  
193 aggregated by averaging to a  $\sim 5.6$  km resolution ( $0.05^\circ$  latitude x  $0.05^\circ$  longitude). Aggregated  
194 rugosity values were highly correlated with the non-aggregated values (slope(se) = 0.872(0.001),  
195  $P < 0.001$ ,  $r^2 = 0.77$ ,  $DF = 148535$ ). Rugosity values were assigned to individual hauls from the  
196 trawl surveys based on location.

197 Grain size was used to characterize seafloor sediment types throughout the sampling area  
198 using the Wentworth Phi ( $\phi$ ) scale, where lower values indicate coarser sediments and higher  
199 values indicate finer sediments. Sediment data were obtained from multiple sources (Table 2)  
200 and mostly consisted of point estimates. Where sediment data in a region had only verbal or  
201 categorical descriptions, these were assigned to Folk codes [47] based on naming conventions in  
202 the U.S. Chart [48]. These were subsequently matched to quantitative sediment estimates using  
203 relationships between grain size, percentage gravel, mud, and sand (%GSM), and Folk codes

204 developed using the full usSEABED database (117,031 point observations) for the Atlantic shelf  
 205 [49], Gulf of Mexico [50], and U.S. West Coast [51]. In the Gulf of Mexico, grain size for each  
 206 polygon was calculated from %GSM using  $\phi$  values for each pure sediment type (e.g., gravel  $\phi =$   
 207  $-2.7$ , sand  $\phi = 1.7$ , and mud  $\phi = 7.5$ ). Point estimates for grain size and %GSM were interpolated  
 208 using inverse distance weighting in the *gstat* package [52, 53] to match the spatial resolution of  
 209 the rugosity data.

210 **Table 2. Sediment data sources.**

Region	Source	Ref	Type	Data
U.S. Atlantic Coast	CONMAP	a	Polygon	Categorical
U.S. Atlantic Coast	ecstdb2005	b	Point	Grain Size; %GSM
Gulf of Mexico	Gulf of Mexico Data Atlas	c	Polygon	%GSM
U.S. West Coast	usSEABED	d	Point	Grain Size; %GSM
Eastern Bering Sea	ebssed	e	Point	Grain Size; %GSM
Gulf of Alaska	Gulf of Alaska Digitization Project	f	Point	Verbal
Aleutian Islands	AFSC	g	Point	Verbal
Gulf of St. Lawrence	Loring and Nota (1973) [54]	h	Digitized polygon map	Categorical
Scotian Shelf; British Columbia; Labrador	Natural Resources Canada Expedition Database	i	Point	Grain Size, %GSM
Newfoundland	Sediment Thickness Database	j	Polygons	Categorical

211 The source and type of data used for quantifying sediment characteristics on different regions of  
 212 the North American continental shelf. Web links to each source are listed below. %GSM  
 213 indicates data consisting of percentage gravel, sand, and mud.

214 <sup>a</sup><http://pubs.usgs.gov/of/2005/1001/data/conmapsg/conmapsg.zip>

215 <sup>b</sup>[http://pubs.usgs.gov/of/2005/1001/data/surficial\\_sediments/ecstdb2005.zip](http://pubs.usgs.gov/of/2005/1001/data/surficial_sediments/ecstdb2005.zip)

216 <sup>c</sup><https://gulfatlas.noaa.gov/>

217 <sup>d</sup><https://pubs.usgs.gov/ds/2006/182/>

218 <sup>e</sup>[data.noaa.gov/dataset/ebssed-database-surficial-sediments-of-the-eastern-bering-sea-continental-shelf](https://data.noaa.gov/dataset/ebssed-database-surficial-sediments-of-the-eastern-bering-sea-continental-shelf)

219 <sup>f</sup><https://www.sciencebase.gov/catalog/item/5699855be4b0ec051295ed8b>

220 <sup>g</sup><http://www.afsc.noaa.gov/RACE/groundfish/Bathymetry/Aleutians.htm>

221 <sup>h</sup><http://www.dfo-mpo.gc.ca/Library/1493.pdf>

222 <sup>i</sup>[http://ed.gdr.nrcan.gc.ca/grainsize\\_e.php](http://ed.gdr.nrcan.gc.ca/grainsize_e.php)

223 <sup>j</sup><http://geogratis.gc.ca/api/en/nrcan-rncan/ess-sst/97fc16ab-aadc-52f5-b33a-9145a78dd21c.html>

224

225

## 226 **Species distribution modeling**

227           To model the observed niche of individual species, we used a two-stage generalized  
228 additive model (GAM) approach [3, 4, 24] with the *mgcv* package in R [55]. GAMs were used  
229 because they require no *a priori* assumptions about the shape of the relationship that a given  
230 species has with a predictor variable and because they allow for nonlinear associations with  
231 habitat features [56]. For each species, models were fitted by using either the combined survey  
232 data from the east coast (including the Gulf of Mexico) or from the west coast U.S., including all  
233 seasons. By including all survey regions and seasons into a single niche model, we were able to  
234 more completely describe the range of thermal conditions in which a species is found [24, 38].  
235 For species occurring on both U.S. coasts, the Atlantic and Pacific Ocean distributions were  
236 modeled separately.

237           For each species, the first-stage GAM was fitted to presence and absence data, and  
238 assumed a binomial error distribution. The second-stage GAM was fitted to log transformed  
239 biomass from non-zero observations and assumed Gaussian errors [3, 4, 24]. Predictor variables  
240 for each model included seasonal bottom and surface temperatures, annual minimum and  
241 maximum bottom temperatures, annual maximum surface temperature, seafloor rugosity and  
242 sediment grain size. Additionally, a categorical indicator for ecological survey was included to  
243 account for differences in sampling gear and methods between surveys (i.e., differences in  
244 survey catchability), which is a common method for standardization of catch data [57, 58]. We  
245 modeled ecological survey as a fixed effect because our data included a majority of the large-  
246 scale continental shelf surveys in North America, as opposed to randomly drawing from a  
247 population of surveys where random effects might be more appropriate. Further, initial trials  
248 indicated that using random effects would greatly increase computer processing time for niche

249 modeling. A majority of the trawl surveys used have had vessel changes during the survey  
250 history or they employ multiple vessels each year. Vessel effects can influence catch and this can  
251 vary among species and years [59]. However, our niche modeling approach did not include  
252 vessel effects in order to reduce model complexity. Thus, our approach assumes that while  
253 catchability may vary among vessels, this variability will appear in the error term and does not  
254 interact with the environmental variables we are interested in. Depth was not included as a  
255 predictor variable so that projections into the future could allow for species to shift into deeper  
256 water [27], which has been observed to occur as a result of ocean warming [3, 4, 14]. Previous  
257 research has indicated that including depth as a predictor would greatly limit the ability of these  
258 models to explain historical shifts in depth, and that models without depth have greater  
259 explanatory power [3]. Further, a majority of the included species had survey observations that  
260 occurred throughout the sampled areas. Thus our approach assumes that any apparent  
261 relationship that species have with depth is driven by temperature variables and seafloor  
262 characteristics. The likelihood of overfitting the GAMs was reduced by including a gamma  
263 setting during model fitting, which acts as a penalty against model complexity. Gamma for each  
264 GAM was set to the log of the number of observations divided by two [56]. Predictions of  
265 biomass from the two-stage GAMs were calculated using the product of the predicted probability  
266 of occurrence and the exponentiated prediction of log-biomass.

267         Several criteria were used to determine which species to include in projections. First, we  
268 limited niche model fitting to species that had at least 250 occurrences within the combined  
269 survey data, which resulted in 703 species that were included for niche modeling. Second, we  
270 fitted a presence-absence model for each species, as described above, to a training data set that  
271 consisted of the initial 80% of hauls that occurred within each region. The remaining 20% of

272 observations were used as a testing data set. The area under the receiver operator curve (AUC)  
 273 was calculated using predicted and observed responses from the testing data with the *dismo*  
 274 package in R [60]. Fourteen species were dropped from the analysis based on AUC scores below  
 275 0.75 [61] and three other species were dropped because observations were restricted to the  
 276 testing data set.

## 277 **Projecting species distributions**

278 Output from sixteen fully coupled general circulation models (GCMs) that participated in  
 279 the Coupled Model Intercomparison Project 5 (CMIP5) were used to generate a range of  
 280 projections for ocean temperature changes over the 21<sup>st</sup> century (Table 3). For each GCM, we  
 281 used output from simulations that were run under two future greenhouse gas emissions scenarios:  
 282 a “strong mitigation” (RCP 2.6) and a “business as usual” scenario (RCP 8.5)[62]. The latter  
 283 predicts continued global warming in excess of 4°C by 2090, while the former is expected to  
 284 lead to global warming that is roughly consistent with the 2°C target of the Paris Agreement  
 285 [17].

286 **Table 3. Climate projection models.**

<b>Model</b>	<b>Modeling Center</b>
bcc-csm1-1-m	Beijing Climate Center, China Meteorological Administration, China
bcc-csm1-1	Beijing Climate Center, China Meteorological Administration, China
CanESM2	Canadian Centre for Climate Modelling and Analysis, Canada
CCSM4	National Centre for Atmospheric Research, U.S.A.
CESM1-CAM5	National Science Foundation, Department of Energy; National Center for Atmospheric Research, U.S.A.
CNRM-CM5	Centre National de Recherches Meteorologiques, France
GFDL-CM3	Geophysical Fluid Dynamics Laboratory, U.S.A.
GFDL-ESM2M	Geophysical Fluid Dynamics Laboratory, U.S.A.
GFDL-ESM2G	Geophysical Fluid Dynamics Laboratory, U.S.A.
GISS-E2-R	NASA Godard Institute for Space Studies, U.S.A.
GISS-E2-H	NASA Godard Institute for Space Studies, U.S.A.
IPSL-CM5A-LR	L'Institut Pierre-Simon Laplace, France
IPSL-CM5A-MR	L'Institut Pierre-Simon Laplace, France
MIROC-ESM	Japan Agency for Marine-Earth Science and Technology; Atmosphere and Ocean Research Institute (The University of Tokyo);

MPI-ESM-LR      National Institute for Environmental Studies, Japan  
NorESM1-ME      Max Planck Institute for Meteorology, Germany  
                         Norwegian Climate Centre, Norway

---

287 The 16 general circulation models used for climate projections including the laboratory of origin.  
288 The spatial resolution of each model can be found at: [https://portal.enes.org/data/enes-model-](https://portal.enes.org/data/enes-model-data/cmip5/resolution)  
289 [data/cmip5/resolution](https://portal.enes.org/data/enes-model-data/cmip5/resolution)

292            Each GCM was first regridded to match the finer spatial resolution of the SODA3.3.1  
293 data (0.25° latitude and longitude at the equator), and the depth strata for projecting bottom  
294 temperatures was refined according to this finer spatial resolution of bathymetry. The delta  
295 method was used to downscale surface and bottom temperatures from the CMIP5 models. For  
296 this procedure, we first calculated the difference (i.e., delta value) between future temperatures  
297 and a modeled baseline period (mean of 1995-2014) with each GCM and for each scenario.  
298 These delta values were then added to a mean temperature climatology developed from the  
299 SODA3.3.1 data for 1995-2014. For the SODA grid cells outside the domain of a CMIP5 model,  
300 we used the nearest CMIP5 grid cell. For a majority of the GCMs ( $N = 12$ ), 5% or less of the  
301 SODA grid cells needed to be populated in this fashion. Four of the GCMs had more restricted  
302 coverage on the continental shelf and between 18 and 35% of grid cells needed to be populated  
303 with neighboring cells. Finally, the climate projection grid was refined to 0.05° latitude x 0.05°  
304 longitude based on the spatial grain of the rugosity and sediment variables. We assumed that  
305 rugosity and sediment variables would be constant for the 21<sup>st</sup> century and predictions were  
306 limited to depths shallower than 401m. Our resulting projection grid for the North American  
307 shelf consisted of 65,826 individual cells on the Pacific coast, 69,209 cells on the Atlantic coast,  
308 and 13,383 cells in the Gulf of Mexico, which was separated from the Atlantic coast at -80.75°  
309 longitude off the southern tip of Florida. For each species, we generated 32 projection series (16  
310 GCMs × 2 RCPs) of annual biomass estimates from 2007 to 2100 for each grid cell during the

311 summer season (July-September). Data from each series were aggregated by averaging  
312 projections within twenty-year bins. Projections ran for 7.7 days on Centauri, a 640-core  
313 computer cluster in the School of Environmental and Biological Sciences at Rutgers University.

## 314 **Analysis and uncertainty estimation**

315 For each species, we calculated the centroid for the present time period (2007-2020) and  
316 the end of the century (2081-2100) for each GCM and RCP. We calculated the centroid as the  
317 predicted biomass-weighted mean latitude and longitude [3]. Projection grid cell areas decline  
318 towards the poles due to converging longitudes and this was factored into centroid calculations  
319 using the *raster* R package [46]. Centroid calculations were conducted separately for the Gulf of  
320 Mexico and the Atlantic coast for species with historic survey observations in both regions.  
321 However, species that only had historic observations in the Gulf of Mexico were analyzed in that  
322 region only. From initial and future centroid locations, we calculated the predicted distance  
323 shifted in km and the direction of the shift in degrees using the *geosphere* R package [63]. The  
324 change in latitudinal centroid was also calculated. We then calculated the mean and standard  
325 deviation among GCM projections within an RCP for distance shifted and change in latitude. We  
326 were not able to calculate shift distances that followed the coastline, as is often done at smaller  
327 spatial scales [14], because there was no simple path northward that spanned our projection grid  
328 on either coast. Centroids were not confined to the projection grid, and for this study, we used  
329 projected shifts in centroids to indicate the magnitude of change in species' distributions.

330 We also calculated a metric for directional agreement among GCM projections by first  
331 converting each projected shift direction into Cartesian coordinates on a unit circle of radius one.  
332 We then averaged these Cartesian coordinates across GCMs and calculated the radius of that  
333 mean position from the origin as an indicator of directional agreement. A radius of zero indicated

334 a complete lack of agreement in shift direction, and a value of one indicated that all GCM  
335 predictions pointed in an identical direction.

336 We used two methods that we termed distance-directional uncertainty (DDU) and  
337 latitudinal uncertainty (LU) to identify which species had relatively robust projections of  
338 distribution changes (strong agreement among models) and which species had poor agreement  
339 among projections. DDU combined metrics for variation in projected shift distance and direction  
340 among the sixteen GCMs. For DDU, we first used linear regression to relate the standard  
341 deviations of shift distance to the mean predicted shift distances (km) of projected species. The  
342 regression was done on a log-log scale to normalize residual errors. We then used the residual  
343 error values from this regression model to indicate the relative uncertainty in shift distance  
344 among species, where positive (negative) residuals indicated projections that were more (less)  
345 uncertain than would be expected given the distance shifted. The residual error values were then  
346 plotted against values for GCM directional agreement. Species falling above the 75<sup>th</sup> percentile  
347 for either the residual error values from the regression or for directional agreement were  
348 considered to have medium uncertainty, while species falling above the 95<sup>th</sup> percentile were  
349 considered to have high uncertainty.

350 Latitudinal uncertainty (LU) was calculated by regressing the standard deviations among  
351 the sixteen GCM predictions against the absolute values of mean predicted shifts in latitude.  
352 This was done on a log-log scale to normalize residual errors. Quantile regression, using the  
353 *quantreg* package in R [64], of the 95<sup>th</sup> and 75<sup>th</sup> percentiles was used to indicate species with  
354 high or medium uncertainty, respectively. For each RCP, species classified as “high uncertainty”  
355 with either the DDU or LU methods were considered to have poor model agreement among  
356 projections, while species with “low uncertainty” for both methods were considered to have

357 robust projections. The low uncertainty species were then used to make comparisons of  
358 assemblage-scale shifts among the major oceanic basins of North America.

359         While centroid calculations reflect spatial patterns of thermal habitat, they do not  
360 elucidate the influence of climate change on the overall amount of thermal habitat available.  
361 Therefore, for each GCM we calculated the projected change in total mean annual thermal  
362 habitat during the 21<sup>st</sup> century. Average annual thermal habitat availability was calculated as the  
363 sum of all projected biomass values (biomass per swept area × grid cell area) from the projection  
364 grid. Predicted change was calculated as a percentage of the mean predicted thermal habitat for  
365 the 2007-2020 period. The mean percentage change in annual thermal habitat of the sixteen  
366 GCMs was calculated for each species that was classified as low uncertainty.

367         Our approach for projecting shifts in species distribution and biomass modeled only the  
368 changes in thermal habitat for each species and did not include other important factors like the  
369 influences of fishing or changes in primary productivity and carbonate chemistry on species  
370 distribution and abundance. In this way, our projections are only projections of potentially  
371 suitable habitats. Interpreting our projections of thermal habitat as projections of species  
372 distributions assumes that species are able to colonize all thermally suitable habitat within our  
373 projection region and that shifts are not limited by reproduction and recruitment dynamics. Our  
374 goal was to isolate temperature effects, and thus provide an indication of the anticipated  
375 magnitude of changes among species and regions as a result of climate change in the 21<sup>st</sup>  
376 century. Further, we use the term ‘thermal habitat availability’ (alt. ‘thermal habitat’) to indicate  
377 that we are not making future predictions of absolute biomass.

378

379

## 380 **Results**

### 381 **Species distribution model summaries and uncertainty analysis**

382 A total of 383 Atlantic species and 303 Pacific species met the criteria during thermal  
383 niche model fitting for conducting projections. This list of species included teleost fishes,  
384 elasmobranchs, three hagfishes, a species of chimaera, a variety of crustaceans, cephalopods,  
385 echinoderms and other invertebrates, and a species of sea turtle (S1 Appendix). The number of  
386 occurrences within the survey data ranged among species from 298 to 35018, with a median  
387 value of 1359 occurrences. The amount of variation in survey data that was explained by the  
388 thermal niche models varied widely by species. For the presence-absence GAMs, all species had  
389 AUC values greater than 0.79, with a median value of 0.94 among species. The percentage of  
390 deviance explained for the presence-absence GAMs ranged from 11.7 to 77.7%, with a median  
391 value of 38.3%. For the logged biomass GAMs, the percentage deviance explained ranged from  
392 3.3 to 98.6% and the median value was 90.0%.

393 Species varied greatly in how much the 16 GCMs agreed in their distribution projections.  
394 The standard deviation of total centroid shift distance among GCMs increased linearly with  
395 mean predicted shift for both RCPs (Fig 2a-b). For the DDU metric, residual values from these  
396 linear relationships were plotted against the directional agreement among GCM predictions (Fig  
397 2c-d). Directional agreement among predictions was much higher for RCP 8.5 projections (75<sup>th</sup>  
398 percentile at 0.72) than for RCP 2.6 (75<sup>th</sup> percentile at 0.41). This difference among RCPs was  
399 primarily due to many species with small projected shift distances under RCP 2.6, which allowed  
400 for more variation in direction among GCMs. The DDU method categorized 498 (507) species  
401 projections as low uncertainty for RCP 2.6 (RCP 8.5), 295 (286) as medium uncertainty, and 85

402 (85) as high uncertainty. Note that some species have separate projections for the east coast and  
403 the Gulf of Mexico, which is why the total exceeds 686 species for each RCP.

404 The standard deviation of predicted latitudinal shifts (positive or negative) of centroids  
405 among GCMs was linearly related to absolute values of the mean predicted shifts in latitude (Fig  
406 2e-f). For categorizing species based on latitudinal uncertainty (LU) for the RCP 2.6 (8.5)  
407 scenario, our method grouped 658 (658) species as low uncertainty, 175 (177) as medium  
408 uncertainty, and 45 (43) as high uncertainty.

409

410 **Fig 2. Species projection uncertainty.** Categorizing uncertainty for 878 species projections  
411 within the RCP 2.6 (A, C, and E) and RCP 8.5 (B, D and F) scenarios. (A and B) The logged  
412 standard deviation of projected shift distance plotted against the logged mean shift distance in  
413 km among 16 GCMs. (C and D) The distance-directional uncertainty (DDU) method where the  
414 residual error values from panels (A) and (B) were plotted against shift directional agreement  
415 among GCMs. (E and F) The latitudinal uncertainty (LU) method where the logged standard  
416 deviation in projected shift in latitude was plotted against logged mean shift in latitude among 16  
417 GCMs. Red and blue lines indicate the 95<sup>th</sup> and 75<sup>th</sup> percentiles (C and D) or quantiles (E and F),  
418 respectively. Points are colored according to their level of uncertainty where red indicates high  
419 uncertainty, orange is medium, and blue is low uncertainty (C–F).

420

421 There was a significant association between our two methods (DDU and LU) for  
422 categorizing species projection robustness (Pearson's Chi-square test for RCP 2.6:  $X_4 = 97.84$ ,  $P$   
423  $< 0.001$ ; RCP 8.5:  $X_4 = 141.4$ ,  $P < 0.001$ ). For RCP 2.6 projections, 59% of species had an  
424 identical uncertainty rating (i.e., high, medium or low) for each method, and for RCP 8.5

425 projections 62% of species had identical ratings. Based on combining DDU and LU methods for  
 426 identifying species with relatively robust projections, for RCP 2.6 (RCP 8.5) we grouped 429  
 427 (448) species as low uncertainty, 329 (314) as medium uncertainty, and 120 (116) as high  
 428 uncertainty (Table 4; S1 Appendix). The level of projection uncertainty for RCP 2.6 was affected  
 429 by how often a species was encountered in survey data (ANOVA:  $F_{2, 875} = 7.714$ ,  $P < 0.001$ ) and  
 430 species in the medium and high uncertainty categories had significantly fewer observations than  
 431 low uncertainty species. Among the RCP 8.5 projections there was no difference in the number  
 432 of survey observations between the low, medium and high uncertainty groups ( $F_{2, 875} = 0.004$ ,  $P$   
 433  $= 0.99$ ).

434

435 **Table 4. Projection uncertainty of species by region.**

Region	RCP 2.6			RCP 8.5		
	Low	Medium	High	Low	Medium	High
Eastern Bering Sea	84	48	12	99	31	14
G. Alaska-W.	71	22	6	61	29	9
Canada						
E. Canada	67	32	12	62	34	15
Northeast U.S.	17	13	8	8	20	10
West U.S.	34	16	10	35	18	7
Southeast U.S.	80	71	36	100	64	23
Gulf of Mexico	76	127	36	83	118	38
<b>Total</b>	429	329	120	448	314	116

436

437 Number of species categorized as low, medium, and high uncertainty within each RCP scenario  
 438 by region.

439

## 440 **Projections of centroid shifts**

441 For presenting the projections of species centroid shifts, we grouped species into seven  
 442 regions based on projected centroid location for the 2007-2020 time period (Figs 3 and 4).  
 443 However, projections for all species were conducted at a coast-wide scale. Under the RCP 2.6  
 444 emissions scenario, the low uncertainty projections of species centroid shifts were generally less

445 than 200 km (Figs 3 and 4). However, multiple projections for RCP 2.6 in the Gulf of Alaska and  
446 West Coast U.S. exceeded 300 km (Fig 3). The magnitudes of shifts were much larger under the  
447 RCP 8.5 scenario, and multiple species shifts exceeded 1500 km on the west coast and exceeded  
448 600 km on the east coast (Figs 3 and 4). Projected shifts generally followed the coastline towards  
449 increasing latitude. For example, species that were primarily caught in the U.S. Northeast Shelf  
450 shifted to the northeast, while species originating from the Gulf of Alaska shifted west and north.  
451 Species from the northernmost regions, such as Eastern Bering Sea and Newfoundland, had  
452 smaller projected shifts, which is probably the result of these regions being constrained by the  
453 northern boundary of our projection region. Projections in the Gulf of Mexico tended to shift  
454 westward or towards the southeast and were generally of lower magnitude, which probably was  
455 the result of this region being constrained by the U.S. coast.

456

457 **Fig 3. Projected shifts in distribution for west coast species.** The direction and magnitude in  
458 km of projected shifts in centroids for 303 species on the North American west coast. Species  
459 were grouped into regions based on projected origin of centroid 2007-2020, but all projections  
460 were on a coast-wide scale. Each regional pair of plots consists of RCP 2.6 projections on the left  
461 and RCP 8.5 projections on the right. Projections colored blue indicate low uncertainty, orange  
462 indicates medium uncertainty, and red indicates high uncertainty. Note that the distance scales on  
463 the compass plots and that of the map do not match. The gray area on the map indicates the  
464 projection area on the continental shelf.

465

466 **Fig 4. Projected shifts in distribution for east coast species.** The direction and magnitude in  
467 km of projected shifts in centroids for 336 species on the North American east coast and 239

468 species in the Gulf of Mexico. For additional detail refer to Figure 3 caption. Note that the scale  
469 of the compass plots for the east and west coasts differ.

470

471         Within regions, there was wide variation in species' projected responses to ocean  
472 warming, both in shift direction and magnitude (Figs 3 and 4). For example, species originating  
473 from the Gulf of Alaska and the west coast of Canada that had low uncertainty projections  
474 ranged in projected shift distance from 267 to 1630 km under RCP 8.5. Generally, projections  
475 among species with low uncertainty had a high level of agreement in shift direction. Although in  
476 some regions, shifts clustered in more than one general direction. For example, in the southeast  
477 many tropical species expanded northward into this region from the Florida shelf, while another  
478 group of species originating from the southeast shifted towards the northeast into the mid-  
479 Atlantic U.S. region. Conversely, shifts in atypical directions for a region were most often  
480 categorized as medium or high uncertainty, illustrating the low level of GCM model agreement  
481 for these species (Figs 3 and 4). West coast projected shifts were generally more robust; in  
482 particular species originating from the Gulf of Alaska and Eastern Bering Sea regions tended to  
483 have robust projections, with both regions having at least 62% of species categorized as low  
484 uncertainty for both RCPs (Table 4). Conversely, in the Gulf of Mexico and Northeast U.S.  
485 regions, less than 45% of species had low uncertainty projected shifts for both RCPs.

486         To compare among regions, we only considered species with low uncertainty projections,  
487 and combined both shift distances and directions to calculate the average assemblage shift for  
488 each region. Under RCP 2.6, the mean shift distance across species was greatest for West Coast  
489 U.S., and Gulf of Alaska and West Coast Canada species (mean shift distance of 224 and 248  
490 km, respectively) (Fig 5a). In contrast, species originating from the Gulf of Mexico and the

491 Southeast U.S. both had mean shifts less than 40 km. For the RCP 8.5 scenario, the highest  
492 magnitude average shifts again occurred for the West Coast U.S. at 1162 km and the Gulf of  
493 Alaska at 954 km, but the Northeast U.S. also had relatively high magnitude projections at 637  
494 km (Fig 5b). Species from the Gulf of Mexico again had the lowest magnitude projected shifts  
495 under RCP 8.5, which partly results from greater variation in projected shift direction among  
496 species (Fig 4).

497

498 **Fig 5. Regional difference in projected distribution shifts.** Mean direction and magnitude of  
499 projected centroid shifts over the 21<sup>st</sup> century for low uncertainty species originating from seven  
500 regions of the North American shelf for (A) RCP 2.6 and (B) RCP 8.5.

501

## 502 **Projections of change in thermal habitat availability**

503 Predicted changes in the availability of thermal habitat over the course of the 21<sup>st</sup> century  
504 were generally of greater magnitude, both positive and negative, for RCP 8.5 predictions as  
505 compared to RCP 2.6 (Fig 6). Many species were projected to experience overall increases in  
506 thermal habitat availability in North America over the 21<sup>st</sup> century, particularly those from the  
507 Southeast, Northeast, and West U.S. Coasts, and the Gulf of Alaska and West Coast of Canada.  
508 These positive responses resulted from two major patterns. First, some species expanded into  
509 regions with larger areas of continental shelf habitat. For example, on the U.S. West coast, both  
510 jack mackerel (*Trachurus symmetricus*) and canary rockfish (*Sebastes pinniger*) had projected  
511 centroid shifts that exceeded 1300 km as they expanded into the Gulf of Alaska and Eastern  
512 Bering Sea, respectively (Fig 7). Associated with these changes in distribution were large  
513 (greater than 90%) predicted increases in thermal habitat availability. The second mechanism by

514 which projections for thermal habitat availability increased was for species of tropical origin that  
515 expanded into the projection area as temperatures increased. Gray snapper (*Lutjanus griseus*)  
516 was initially most abundant west of Florida, but its thermal habitat expanded throughout the Gulf  
517 of Mexico (71% increase; Fig 8). In the Southeast U.S. shelf gray snapper was initially projected  
518 to have negligible habitat, and so the expansion of this species into the region by the end of the  
519 21<sup>st</sup> century led to a large estimate of increase in thermal habitat (96,663% increase), which was  
520 a common trend in this region (Fig. 6).

521 Not all species that expanded northward had major increases in thermal habitat  
522 availability. Sheepshead (*Archosargus probatocephalus*) was projected to shift northward on the  
523 east coast by 2.4 degrees of latitude, but a 46% decline in total suitable habitat was predicted for  
524 this species because habitat gained in the Northeast U.S. shelf was still marginal (Fig 8).  
525 Temperatures became less favorable in the Gulf of Mexico for sheepshead resulting in a loss of  
526 83% of initial habitat. The projected loss in habitat for sheepshead within the Gulf of Mexico  
527 was among the medium uncertainty group, despite having a low uncertainty projection on the  
528 Atlantic coast. Nevertheless, 43% of Gulf of Mexico species with robust projections also lost  
529 thermal habitat during the 21<sup>st</sup> century (Fig. 6). Spiny dogfish (*Squalus acanthias*) was projected  
530 to have an increase in habitat suitability during the 21<sup>st</sup> century in areas of the Newfoundland  
531 shelf and in the Gulf of St. Lawrence as the center of distribution shifted 483 km (Fig 8).  
532 However, spiny dogfish was predicted to have a 32% net loss of thermal habitat coast-wide due  
533 to a major decline in habitat availability in the southern half of its range.

534 Species common to the northern extreme areas of the Eastern Bering Sea and Eastern  
535 Canada shelf generally had negative trends in thermal habitat availability within our study region  
536 (Fig 6). The large predicted loss of thermal habitat for these northern species may partly result

537 from their distributions moving out of our projection area. For example, walleye pollock  
538 (*Theragra chalcogramma*) was initially abundant throughout the Alaskan shelf, but by the end of  
539 the century it experienced a loss of 44% of thermal habitat and was projected to be largely  
540 restricted to the Eastern Bering Sea at reduced densities (Fig 7).

541

542 **Fig 6. Projected change in thermal habitat availability.** Mean percentage change in projected  
543 thermal habitat availability over the 21<sup>st</sup> century for low uncertainty species originating from  
544 seven regions of the North American shelf for (A) RCP 2.6 and (B) RCP 8.5. Boxes indicate the  
545 median and the 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers extend to within 1.5 of the interquartile range  
546 or to data extremes. Number of extreme data points occurring out of the plotting range is  
547 indicated for each region at the top. The right y-axis in (B) applies to SE U.S. only. Sample size  
548 for each region is provided in Table 4.

549

550 **Fig 7. Examples of west coast species projections.** Jack mackerel *Trachurus symmetricus* is in  
551 the left-most column, canary rockfish *Sebastes pinniger* is in the middle column, and walleye  
552 pollock *Theragra chalcogramma* is in the right-most column. Mean annual thermal habitat  
553 suitability during summer under RCP 8.5 is shown for twenty-year periods in the 21<sup>st</sup> century.  
554 Habitat quality is higher in areas of greater blue intensity. Gray areas indicate regions of the  
555 projection grid that are not suitable thermal habitat. White areas indicate regions not included in  
556 the projections (either land or deep water).

557

558 **Fig 8. Examples of east coast species projections.** Gray snapper *Lutjanus griseus* is in the left-  
559 most column, sheepshead *Archosargus probatocephalus* is in the middle column, and spiny

560 dogfish *Squalus acanthias* is in the right-most column. For other details, refer to Figure 7  
561 caption.

562

## 563 **Discussion**

564 Water temperature is a major factor in determining the geographic distribution and  
565 preferred habitats of marine species, though the mechanism for these relationships is perhaps  
566 mediated by oxygen demand and availability [1, 3, 65, 66]. We have shown that climate change  
567 in the 21<sup>st</sup> century will shift the location and available area of suitable thermal habitat for species  
568 inhabiting the North American shelf. These shifts in thermal habitat can interact in complex  
569 ways with seafloor characteristics and variations in the width of the continental shelf to produce  
570 a wide range of predicted species responses. Despite this strong variation among species and  
571 among climate models, the general trend was for poleward shifts in thermal habitat, which is  
572 similar to previous studies predicting changes in species distribution [23-25, 28, 29]. However,  
573 most previous studies have either taken a more regional approach to species projections and  
574 focused on changes in available habitat within the bounds of a biological survey, or have taken a  
575 coarse global approach. Here we have presented some of the first fine-grained projections for  
576 distribution changes that encompass the majority of the geographic ranges for hundreds of  
577 marine species in North America.

578 There are few existing studies that have also projected species distribution shifts at a  
579 larger geographic scale. Robinson et al. [23] found a mean projected poleward shift of ~400 km  
580 under a high emissions scenario for a group of nine pelagic species off eastern Australia by the  
581 year 2070. Our projection summaries were for the end of the 21<sup>st</sup> century, but the projected shift  
582 distances from many of our regional assemblages were similar to Robinson et al. [23]. Cheung et

583 al. [25] conducted projections for 1066 species globally and found that the median projected  
584 poleward shift of the center of marine species' ranges was 79 km for a high carbon emissions  
585 scenario. This study projected shifts between 2000-2005 and 2040-2060 and used a single  
586 climate projection model. Further, the bioclimate envelope models used to project distribution  
587 shifts in their study were different than our approach, and incorporated population dynamics such  
588 as dispersal and population growth. Nevertheless, when we made a similar calculation for  
589 poleward shifts in latitudinal centroid among our projected species we found a median value of  
590 164 km (~20.6 km per decade). Simple comparisons between our results and Cheung et al. [25]  
591 are difficult to make for multiple reasons (e.g., different species and regions examined, different  
592 climate models used), but considering that our projections are to the years 2081-2100, then the  
593 median latitudinal shift values between our studies are similar. More recently, Jones and Cheung  
594 [67] projected distribution shifts on a global scale for 802 marine species and compared three  
595 different approaches of presence-only niche modeling, using a single climate projection model.  
596 They found a median poleward shift of 25.6 km per decade for species centroids under RCP 8.5,  
597 which is similar to our value of ~20.6 km for North American species. While similarities among  
598 results from these projection studies are encouraging, there is still a poor understanding of how  
599 these different approaches to species niche modeling influence projections [34].

600 Species from the U.S. West Coast, Gulf of Alaska and West Canada Coast assemblages  
601 had relatively large predicted shifts in distribution, some exceeding 1500 km for the high  
602 emissions scenario (RCP 8.5). It is challenging to assess the realism of these projections by  
603 looking at historic trends in marine species distribution shifts, largely because available historical  
604 data are typically restricted to a region. However, even at a regional scale species distribution  
605 shifts greater than 10 km per year have been observed [3, 68], which would scale to 1000 km

606 over a century. Further, ocean warming rates under the RCP 8.5 scenario are projected to be  
607 greater than what has been observed during the past four decades, the decades during which most  
608 long-term surveys were operational [69]. This suggests that our projections are likely consistent  
609 with historical observations.

610         The dramatic predictions for centroid shifts for Pacific species (excluding Eastern Bering  
611 Sea) might be expected because the spatial gradient of temperature change on the west coast is  
612 much weaker than on the east coast [12]. Consequently, the projected climate velocity (the rate  
613 and direction of isotherm shift) on the west coast of North America is predicted to have a much  
614 stronger along-shore and poleward trajectory than on the east coast [70]. This is important  
615 because predicted shifts in species distribution can be greater in areas with weak spatial gradients  
616 in temperature change [23]. Another reason for the large magnitude shifts among Pacific species  
617 is the greater continental shelf habitat available to the north. In other words, as habitat becomes  
618 suitable at latitudes corresponding to the Gulf of Alaska or Eastern Bering Sea, the greater  
619 amount of continental shelf in these regions results in major thermal habitat increases, which  
620 strongly influenced estimates for geographic centers of biomass.

621         Interestingly, the projected shifts of marine species for the U.S. West assemblage  
622 represented a contrast to historic trends in this area, where ocean temperatures have been  
623 relatively static or even cooling in recent decades [12]. Consequently, the distribution of species  
624 in this region has been relatively stable compared to other North American areas [3]. Our  
625 predictions show a similar contrast for the Southeast U.S., where temperatures and species  
626 distributions have also been relatively static in recent decades [9], but where our projections  
627 suggested rapid northward shifts in the future.

628 Species common to the northern parts of our projection area had lower magnitude  
629 projections for shift distance, and projections for changes in thermal habitat availability were  
630 generally negative. However, many of these species may be able to redistribute northwards and  
631 out of our study region, where continental shelf habitat is also available. For example, in the  
632 Barents Sea, more temperate Atlantic species have been spreading into areas where seasonal sea  
633 ice occurs, displacing Arctic species [71]. We did not extend our projection grid towards Arctic  
634 waters due to a lack of biological survey data in these regions, along with a lack of data on  
635 sediment characteristics. However, Wisz et al. [72] used niche habitat modeling for north  
636 Atlantic and Pacific species and projected that Arctic regions will become suitable for many  
637 temperate species during the 21st century.

638 Predicted shift distances were also small in the Gulf of Mexico and there was the least  
639 agreement in shift direction among the low uncertainty species. This may be unsurprising as  
640 temperatures are more uniform across the Gulf of Mexico compared to other regions of the North  
641 American shelf, and there was not a strong along-shore directional gradient in our temperature  
642 climatology for this region. Further, projected isotherm shifts in this region are generally  
643 poleward as opposed to along shore [70]. As a result, shifts in this region were often driven by  
644 tropical species expanding throughout the region (e.g., gray snapper, Fig 8) or by species  
645 generally losing habitat (e.g., sheephead, Fig 8). Also, some species were projected to become  
646 increasingly restricted to deeper habitats, which has been shown with historic observations from  
647 survey data [3, 4].

648 Despite the detailed data that went into our species distribution models, the models were  
649 fitted in an automated fashion and did not account for a detailed understanding of each species'  
650 natural history. However, the benefit of an automated approach to model fitting is that we could

651 make projections for a wide range of species. A closer examination of gray snapper (Fig 8) helps  
652 to illuminate the caveats of this approach. Climate change impacts for this species have been  
653 studied in detail, and so this offers a good opportunity for comparison. Hare et al. [29] predicted  
654 gray snapper to be resident on the U.S. Southeast coast to a maximum extent of between 31 and  
655 31.5° N by the end of the century for a high greenhouse gas emissions scenario. Their study  
656 projected gray snapper distributions based on low temperature tolerance during winter through  
657 effects on overwinter survival in estuaries. Similarly, minimum annual bottom water  
658 temperatures were an important predictor for our gray snapper niche model. However, we  
659 predicted gray snapper to extend to ~34° N under RCP 8.5. This difference between studies  
660 suggests the importance of recruitment dynamics. Gray snapper are estuarine dependent and  
661 early life stages occur close to shore [29]. Indeed, a close inspection of our projection for gray  
662 snapper at the end of the century indicated that above ~31.5° N, gray snapper were excluded  
663 from the shallowest areas of the shelf, where winter temperatures were relatively low. The  
664 process our model does not capture is that excluding gray snapper from the shallowest parts of  
665 the shelf also excludes the adults from the same latitude further offshore [29, 73]. However, our  
666 results are surprisingly consistent with Hare et al. [29] when examining nearshore habitat on the  
667 shelf, despite our two studies using very different niche modeling approaches.

668

## 669 **Uncertainty in species projections**

670 The magnitude and direction of projected shifts in distribution varied widely among  
671 species, but we also found variation in the robustness of projections. We used sixteen different  
672 GCMs for species projections so as to examine a range of possible temperature futures within  
673 each RCP. While each of these GCMs predict global ocean warming under both greenhouse gas

674 scenarios, they vary significantly in the magnitude of their predictions, particularly at a regional  
675 scale [35]. Uncertainty among GCM predictions is higher at the smaller spatial scales at which  
676 predictions of living marine resource responses to climate are generally made [22, 34, 35].  
677 Therefore, major differences in species predictions can occur when using different GCMs.  
678 Calculating a mean response from multiple projections reduces the bias from any one model and  
679 also allows the calculation of variance around projections [22, 23, 29]. However, the amount of  
680 variation among GCM projections can be difficult to put into context without comparing across  
681 species. Our results for projections of 686 species suggest that results for some species may be  
682 unreliable based on poor model agreement. Therefore, there are major benefits in conducting  
683 projections with many species under a similar framework, because less robust projections can be  
684 down-weighted during interpretation of general trends.

685         Our method for identifying robust projections was based on two metrics that quantified  
686 the distance-directional and latitudinal uncertainty in projected shifts. These two metrics were  
687 used, as opposed to using only one, in order to maximize our ability to identify species with  
688 greater uncertainty so that regional assemblages could be compared using only robust  
689 projections. Further, we did not assess if one metric for uncertainty is more robust than the other.  
690 Indeed, some species had different ratings for uncertainty between these two metrics, suggesting  
691 that one method to characterize uncertainty may not always be adequate. The uncertainty metrics  
692 were essentially based on a ranking of species' model agreement (i.e., quantiles) and were  
693 somewhat arbitrary in that we chose the 95<sup>th</sup> and 75<sup>th</sup> percentiles to indicate high and medium  
694 uncertainty species, respectively. However, this framework nonetheless provided an objective  
695 way to omit less robust projections for analyses of regional trends.

696 Most of the regional assemblages had at least some unexpected projections (e.g.,  
697 equatorward shifts in the East Canada region) and our metrics for uncertainty indicated that these  
698 were generally less robust. However, we note that our uncertainty methods were potentially  
699 conservative, and some species categorized with medium or high uncertainty may still have  
700 useful predictions. Further, some regions may have been more likely to have medium or high  
701 uncertainty projections based on the coastal geometry and climatology. For example, species  
702 originating from the Northeast U.S. were generally shifting into a large area of continental shelf  
703 (e.g., Gulf of St. Lawrence and the Grand Banks) and so the potential for variation among GCM  
704 predictions was greater there. Similarly, shifts in the Gulf of Mexico were particularly sensitive  
705 to the DDU metric (only 38% had low uncertainty for DDU), which probably arises from the  
706 lack of a strong along-shore direction in climate velocity, as discussed above. For example,  
707 sheephead (Fig 8) were considered medium uncertainty in the Gulf of Mexico because of the  
708 DDU metric, but all 16 GCMs predicted 64% or greater loss in thermal habitat during the 21<sup>st</sup>  
709 century for this species. In addition to considering potential regional biases in our uncertainty  
710 metrics, it was also apparent that the level of agreement in projections among the 16 GCMs  
711 varied spatially for some species. Thus, even species considered to have high uncertainty  
712 projections at the coastwide scale, may still have strong agreement among GCMs within portions  
713 of their ranges. This may occur when projections vary more at species range edges than in core  
714 areas of distributions. This indicates potential threshold effects [34], where a portion of GCMs  
715 predict temperature changes that exceed a limiting value and cause a shift or expansion in the  
716 distribution of a species, which leads to greater uncertainty among GCMs. Therefore, projection  
717 uncertainty may depend on the spatial scale of interest, and for this study we have focused on  
718 coastwide predictions.

719 Atlantic cod (*Gadus morhua*) are an example of a species with useful projection results at  
720 a regional scale, despite not being grouped with low uncertainty projections. This species was  
721 generally predicted to occur throughout the north Atlantic, with a southern limit in the Gulf of  
722 Maine and Georges Bank during 2007-2020. Atlantic cod was considered medium uncertainty  
723 due to relatively high variability in the extent of latitudinal shift among GCMs (i.e., latitudinal  
724 uncertainty). Nevertheless, there was strong agreement among the GCMs for a southern range  
725 contraction. There was a 90.7% mean (16.1% s.d.) projected loss of thermal habitat for Atlantic  
726 cod in U.S. waters, which includes the Gulf of Maine and Georges Bank, during the 21st century  
727 under RCP 8.5; thirteen out of the sixteen GCMs that we used projected a greater than 90% loss  
728 for this region. Similarly, Kleisner et al. [24] modeled historic and future abundance of Atlantic  
729 cod in the Northeast U.S. region based on a climate projection model that had a higher resolution  
730 than any of the 16 GCMs in our study [18]. Their results also indicated that thermal habitat in  
731 this region will become unsuitable for cod during the 21st century, which was consistent with  
732 historical trends of habitat loss [24]. Thus, our medium or high uncertainty species projections  
733 may still be useful to resource management depending on the spatial context. Similarly,  
734 projected shifts in thermal habitat may differ between coastwide trends, as we reported in our  
735 study, and subregions within a species geographic range. For example, Kleisner et al. [4] showed  
736 that historic species shifts in latitude and depth can vary among major regions of the continental  
737 shelf. Therefore, it is important for resource managers to consider projected changes in thermal  
738 habitat at coastwide and regional scales.

739 Our results incorporated two major sources of uncertainty that may affect future climatic  
740 conditions, namely scenario uncertainty of future greenhouse gas concentrations (RCP 2.6 versus  
741 RCP 8.5), and model uncertainty among climate projections (i.e., 16 GCMs). We did not include

742 uncertainty from natural internal variability within GCMs—which can affect predicted outcomes  
743 of ocean temperatures [34, 35]—because variation among different GCMs was expected to be  
744 greater on decadal to centennial timescales [35]. Among the 16 GCMs that we used for  
745 projections, the horizontal and vertical resolution varied, along with the extent of spatial  
746 coverage on the continental shelf. However, all of these climate models projected ocean  
747 temperature changes at a relatively coarse grain (i.e., 0.25° latitude and longitude or greater),  
748 which does not allow for precise representation of mesoscale ocean features (e.g., ocean eddies  
749 or upwelling dynamics), complex bathymetry (e.g., deep-water channels), or shallow-coastal  
750 areas of the continental shelf [18]. Despite the relatively coarse resolution, IPCC-class global  
751 climate models like the ones we used have been widely used to study future changes in  
752 upwelling regions, including the finding that the locations of prominent upwelling regions are  
753 expected to shift poleward in the 21st century [74] and that anthropogenic trends in upwelling  
754 will merge primarily in the second half of this century [75]. Presently, high resolution (e.g., 10  
755 km horizontal grain) climate projection models that can be run on centennial timescales are rare  
756 and present limited opportunities for ensemble modeling [18]. However, as more high resolution  
757 GCMs become available, an examination of how climate model resolution impacts the projected  
758 response of marine species would be valuable.

759         Another source of uncertainty that we did not address is associated with species habitat  
760 model structure [34]. Previous research has suggested that the structure of habitat models can  
761 affect predicted outcomes [67, 76]. Robinson et al. [23] used two types of thermal habitat  
762 modeling frameworks for projecting distribution shifts for a group of pelagic fishes. They found  
763 differences between the two model types, but uncertainty between model types was generally  
764 lower than that attributed to climate projection uncertainties. Parameter uncertainty may also

765 influence predicted outcomes. Hare et al. [29] show that uncertainty in thermal tolerance in gray  
766 snapper was the primary source of projection uncertainty. Generally, our niche models  
767 performed well at the coast-wide scale in terms of the amount of variation explained (i.e., percent  
768 deviance) in the trawl catch data. Further, the presence-absence models had high predictive  
769 power when applied to independent testing data (median AUC: 0.93). Nevertheless, a modeling  
770 structure that, for example, accounted for individual vessel effects [57] or spatial autocorrelation  
771 [77] might refine parameter values. There is still a relatively poor understanding for how these  
772 habitat model uncertainties might affect projections and how these uncertainties vary among  
773 species [34]. Future work will be devoted to quantifying habitat model uncertainties with a  
774 subset of the species analyzed here.

## 775 **Implications for the management of living marine resources**

776 Our results contribute to a growing body of work that stresses the importance of the level  
777 of global warming for the magnitude of changes in living marine resources by the end of this  
778 century. We found dramatic differences in the magnitude of distribution and thermal biomass  
779 changes between RCP 2.6 and 8.5. These major difference result from only about 2 to 3°C global  
780 warming difference [17]. Marine species responses to temperature are often nonlinear, and so  
781 small increases in temperature can have large impacts on predicted outcomes [29, 66, 78]. A high  
782 greenhouse gas emissions scenario has been predicted to have large impacts on regional  
783 biodiversity [32] and a net loss in fisheries productivity in most coastal regions of North America  
784 [79]. Our results add to this and suggest that a future under a ‘business-as-usual’ greenhouse gas  
785 emissions scenario (i.e., RCP 8.5) will lead to large shifts in the distribution of species important  
786 to fisheries. These shifts in turn may lead to a host of management challenges, including shifts in  
787 fishing locations [80], conflict over regional allocation of fisheries quota, displaced fisherman,

788 and changes in stock boundaries [81, 82]. However, if emissions are curtailed to a level that is  
789 consistent with the Paris Agreement (i.e., RCP 2.6), then dramatic shifts in species distribution  
790 can be mostly avoided.

791 A primary motivation for producing these species projections was to contribute to a set of  
792 tools available to policy makers and managers considering climate adaptation of marine fisheries  
793 management. In the United States, fisheries are managed regionally, including species that are  
794 managed by individual states and federally managed fisheries that are governed by regional  
795 councils with representatives from neighboring states. Existing tools for climate adaptation in  
796 fisheries management include descriptions of historical species distribution shifts from biological  
797 survey data [3], expert judgment climate vulnerability assessments for marine species [20], and  
798 social vulnerability assessments [83]. The projections produced here can also help regional  
799 managers identify species that are most likely to experience major changes in availability to  
800 fisheries. At the regional management scale, there will be fisheries that experience negative  
801 consequences of ocean warming, but also potentially positive outcomes when valuable species  
802 expand into an area [24]. As the availability of species shift, coordination among regional  
803 management groups will be critically important, and the projections summarized here may offer  
804 an objective tool for management groups to begin communication prior to conflict over, for  
805 example, regional allocation [82]. Further, these projections can be utilized for future efforts to  
806 assess the risk of shifting fisheries for different coastal communities [83].

807

## 808 **Acknowledgments**

809 We acknowledge the World Climate Research Programme's Working Group on Coupled  
810 Modelling, which was responsible for CMIP5, and we thank the climate modeling groups for

811 producing and making available their model output. For CMIP5, the U.S. Department of  
812 Energy's Program for Climate Model Diagnosis and Intercomparison provided coordinating  
813 support and led development of software infrastructure in partnership with the Global  
814 Organization for Earth System Science Portals. For helpful discussions: Roger Griffis, Jon Hare,  
815 Enrique Curchitser, Ryan Batt, Mike Fogarty, and Sean Lucey. We thank two anonymous  
816 reviewers for their useful input, which greatly improved this manuscript.

817

## 818 **References**

- 819 1. Sunday JM, Bates AE, Duty NK. Thermal tolerance and the global redistribution of  
820 animals. *Nat Clim Chang*. 2012; 2:686-690.
- 821 2. Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, et al.  
822 Global imprint of climate change on marine life. *Nat Clim Chang*. 2013; 3:919-925.
- 823 3. Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. Marine taxa track local  
824 climate velocities. *Science*. 2013; 341:1239-1242.
- 825 4. Kleisner KM, Fogarty MJ, McGee S, Barnett A, Fratantoni P, Greene J, et al. The effects  
826 of sub-regional climate velocity on the distribution and spatial extent of marine species  
827 assemblages. *PloS ONE*. 2016; 1-21.
- 828 5. Hettler WF. Correlation of winter temperature and landings of pink shrimp *Penaeus*  
829 *duorarum* in North Carolina. *Fish Bull*. 1992; 90:405-406.
- 830 6. Meng KC, Oremus KL, Gaines SD. New England cod collapse and the climate. *PloS*  
831 *ONE*. 2016; 11:1-10.
- 832 7. Sims DW, Genner MJ, Southward AJ, Hawkins SJ. Timing of squid migration reflects  
833 north Atlantic climate variability. *Proc Roy Soc Lon B*. 2001; 268:2607-2611.
- 834 8. Mills KE, Pershing AJ, Brown CJ, Chen Y, Chiang F-S, Holland DS, et al. Fisheries  
835 management in a changing climate: Lessons from the 2012 ocean heat wave in the  
836 northeast Atlantic. *Oceanog*. 2013; 26(2):191-195.
- 837 9. Morley JW, Batt RD, Pinsky ML. Marine assemblages respond rapidly to winter climate  
838 variability. *Glob Chan Bio*. 2017; 23:2590-2601.
- 839 10. Cheung WWL, Watson R, Pauly D. Signature of ocean warming in global fisheries catch.  
840 *Nature*. 2013; 497:365-368.
- 841 11. Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Zeller D, et al. Large-  
842 scale redistribution of maximum fisheries catch potential in the global ocean under  
843 climate change. *Glob Chan Bio*. 2010; 16:24-35.
- 844 12. Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, et al.  
845 The pace of shifting climate in marine and terrestrial ecosystems. *Science*. 2011;  
846 334:652-655.
- 847 13. Pershing AJ, Alexander MA, Hernandez CM, Kerr LA, Bris AL, Mills KE, et al. Slow  
848 adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod  
849 fishery. *Science*. 2015; 350:809-812.

- 850 14. Nye JA, Link JS, Hare JA, Overholtz WJ. Changing spatial distribution of fish stocks in  
851 relation to climate and population size on the northeast United States continental shelf.  
852 Mar Eco Prog Ser. 2009; 393:111-129.
- 853 15. Miller KA, Munro GR. Climate and cooperation: a new perspective on the management  
854 of shared fish stocks. Mar Res Eco. 2004; 19:367-393.
- 855 16. Bell RJ, Richardson DE, Hare JA, Lynch PD, Fratantoni PS. Disentangling the effects of  
856 climate, abundance, and size on the distribution of marine fish: an example based on four  
857 stocks from the northeast US shelf. ICES J Mar Sci. 2015; 72(5):1311-1322.
- 858 17. Collins M, Knutti R, Arblaster J, Dufresne J-L, Fichetef T, Friedlingstein P, et al. Long-  
859 term Climate Change: Projections, Commitments and Irreversibility, Climate Change  
860 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth  
861 Assessment Report of the Intergovernmental Panel on Climate Change. 2013.  
862 doi:10.1017/CBO9781107415324.024.
- 863 18. Saba VS, Griffies SM, Anderson WG, Winton M, Alexander MA, Delworth TL, et al.  
864 Enhanced warming of the northeast Atlantic ocean under climate change. J Geophys Res:  
865 Ocean. 2016; 121:118-132.
- 866 19. Shackell NL, Greenan BW, Pepin P, Chabotand D, Warburton A. Climate Change  
867 Impacts, Vulnerabilities and Opportunities Analysis of the Marine Atlantic Basin. Can  
868 Manusc Rep Fish Aquat Sci. 2013; 3012. 366p.
- 869 20. Hare JA, Morrison WE, Nelson MW, Stachura MM, Teeters EJ, Griffis RB, et al. A  
870 vulnerability assessment of fish and invertebrates to climate change on the northeast U.S.  
871 continental shelf. PloS ONE. 2016; 1-30.
- 872 21. Busch DS, Griffis R, Link J, Abrams K, Baker J, Brainard RE, et al. Climate science  
873 strategy of the US national marine fisheries service. Mar Pol. 2016; 74:58-67.
- 874 22. Stock CA, Alexander MA, Bond NA, Brander KM, Cheung WWL, Curchitser EN, et al.  
875 On the use of IPCC-class models to assess the impact of climate on Living Marine  
876 Resources. Prog Oceanog. 2011; 88:1-27.
- 877 23. Robinson LM, Hobday AJ, Possingham HP, Richardson AJ. Trailing edges projected to  
878 move faster than leading edges for large pelagic fish habitats under climate change.  
879 Deep-sea Res II. 2015; 113:225-234.
- 880 24. Kleisner KM, Fogarty MJ, McGee S, Hare JA, Moret S, Perretti CT, et al. Marine species  
881 distribution shifts on the U.S. northeast continental shelf under continued ocean warming.  
882 Prog Oceanog. 2017; 153:24-36.
- 883 25. Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D. Projecting  
884 global marine biodiversity impacts under climate change scenarios. Fish Fisheries. 2009;  
885 10:235-251.
- 886 26. Rutterford LA, Simpson SD, Jennings S, Johnson MP, Blanchard JL, Schon P-J, et al.  
887 Future fish distributions constrained by depth in warming seas. Nat Clim Chang. 2015;  
888 5:569-573.
- 889 27. Hare JA, Manderson JP, Nye JA, Alexander MA, Auster PJ, Borggaard DL, et al. Cusk  
890 (*Brosme brosme*) and climate change: assessing the threat to a candidate marine fish  
891 species under the US Endangered Species Act. ICES J Mar Sci. 2012; 69(10):1753-1768.
- 892 28. Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, et al.  
893 Predicted habitat shifts of Pacific top predators in a changing climate. Nat Clim Chang.  
894 2013; 3:234-238.

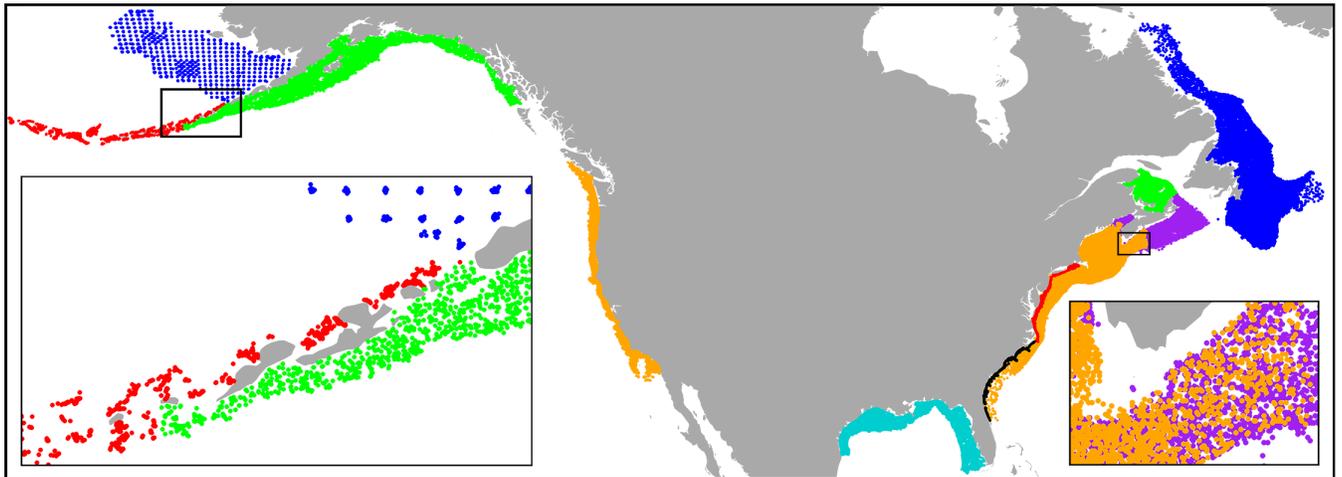
- 895 29. Hare JA, Wuenschel MJ, Kimball ME. Projecting range limits with coupled thermal  
896 tolerance-climate change models: an example based on gray snapper (*Lutjanus griseus*)  
897 along the U.S. east coast. PloS ONE. 2012; 7:1-13.
- 898 30. Grieve BD, Curchitser EN, Rykaczewski RR. Range expansion of the invasive lionfish in  
899 the Northwest Atlantic with climate change. Mar Eco Prog Ser. 2016; 546:225-237.
- 900 31. Hare JA, Alexander MA, Fogarty MJ, Williams EH, Scott JD. Forecasting the dynamics  
901 of a coastal fishery species using a coupled climate-population model. Ecol App. 2010;  
902 20:452-464.
- 903 32. Molinos JG, Halpern BS, Schoeman DS, Brown CJ, Kiessling W, Moore PJ, et al.  
904 Climate velocity and the future redistribution of marine biodiversity. Nat Clim Chang.  
905 2016; 6:83-88.
- 906 33. Planque B, Bellier E, Loots C. Uncertainties in projecting spatial distributions of marine  
907 populations. ICES J Mar Sci. 2011; 68(6):1045-1050.
- 908 34. Cheung WWL, Frölicher TL, Asch RG, Jones MC, Pinsky ML, Reygondeau G, et al.  
909 Building confidence in projections of the responses of living marine resources to climate  
910 change. ICES J Mar Sci. 2016; 73(5):1283-1296.
- 911 35. Frölicher TL, Rodgers KB, Stock CA, Cheung WWL. Sources of uncertainties in 21st  
912 century projections of potential ocean ecosystem stressors. Glob Biogeochem Cyc. 2016;  
913 30(8):1224–1243. doi:10.1002/2015GB005338, 2015GB005338.
- 914 36. Cheung WWL, Jones MC, Reygondeau G, Stock CA, Lam VWY, Frölicher TL.  
915 Structural uncertainty in projecting global fisheries catches under climate change. Ecol  
916 Mod. 2016; 325:57-66.
- 917 37. Batt RD, Morley JW, Selden RL, Tingley MW, Pinsky ML. Gradual changes in range  
918 size accompany long-term trends in species richness. Ecol Lett. 2017. doi:  
919 10.1111/ele.12812.
- 920 38. Selden RL, Batt RD, Saba VS, Pinsky ML. Diversity in thermal affinity among key  
921 piscivores buffers impacts of ocean warming on predator-prey interactions. Glob Chan  
922 Bio. 2018; 24:117-131.
- 923 39. R Core Team. R: A language and environment for statistical computing. R Foundation  
924 for Statistical Computing, Vienna, Austria. 2016. <http://www.R-project.org/>.
- 925 40. Jones MC, Dye SR, Pinnegar JK, Warren R, Cheung WWL. Modelling commercial fish  
926 distributions: prediction and assessment using different approaches. Ecol Mod. 2012;  
927 225:133-145.
- 928 41. Carton JA, Chepurin GA, Chen L. An updated reanalysis of ocean climate using the  
929 Simple Ocean Data Assimilation version 3 (SODA3), manuscript in preparation. 2016.
- 930 42. Dana JD. On an isothermal oceanic chart, illustrating the geographical distribution of  
931 marine animals. Am. J. Sci. Arts, 2d ser. 1853; 66:153-392.
- 932 43. Stuart-Smith RD, Edgar GJ, Bates AE. Thermal limits to the geographic distributions of  
933 shallow-water marine species. Nat Eco Evo. 2017; 1:1846-1852.
- 934 44. Methratta ET, Link JS. Seasonal variation in groundfish habitat associations in the Gulf  
935 of Maine-Georges Bank region. Mar Eco Prog Ser. 2006; 326:245-256.
- 936 45. Becker JJ, Sandwell DT, Smith WHF, Braud J, Binder B, Depner J, et al. Global  
937 Bathymetry and Elevation Data at 30 Arc Seconds Resolution: SRTM30\_PLUS. Mar  
938 Geod. 2009; 32:355–372. doi: 10.1080/01490410903297766.
- 939 46. Hijmans RJ. raster: Geographic Data Analysis and Modeling. R package version 2.3-40.  
940 2015. <http://CRAN.R-project.org/package=raster>.

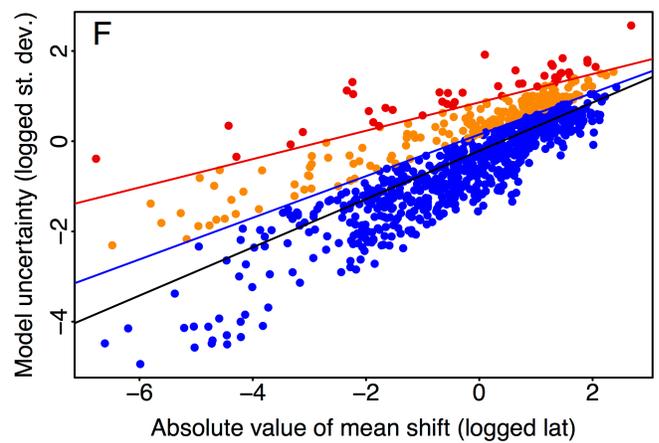
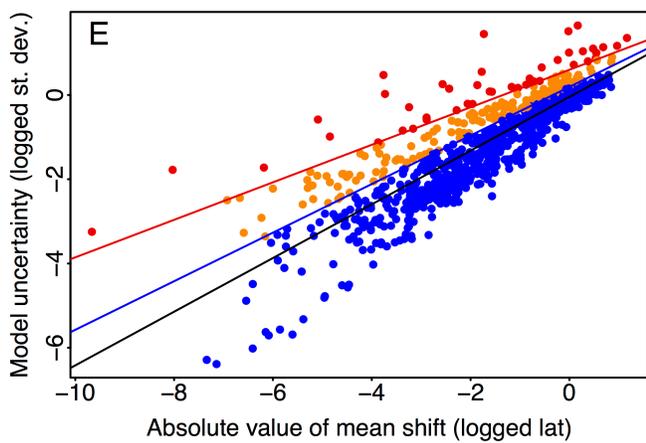
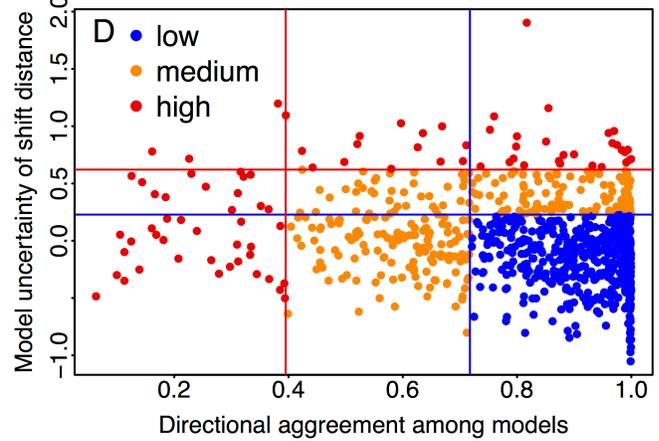
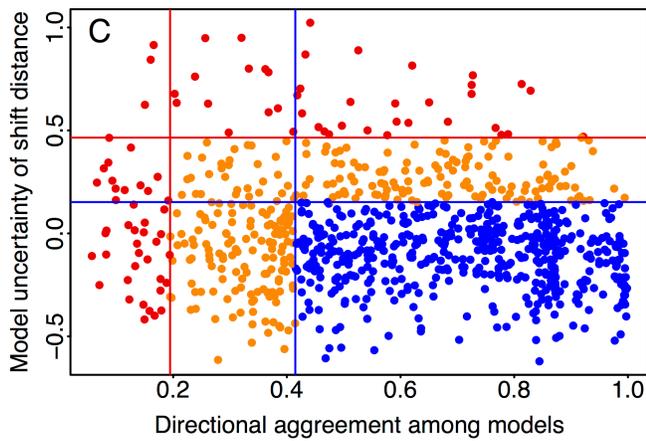
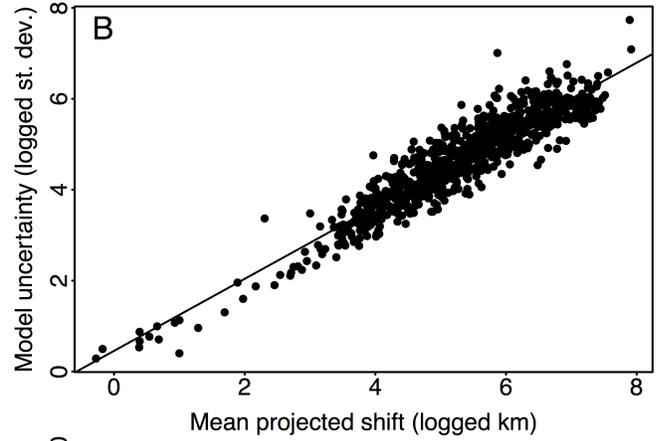
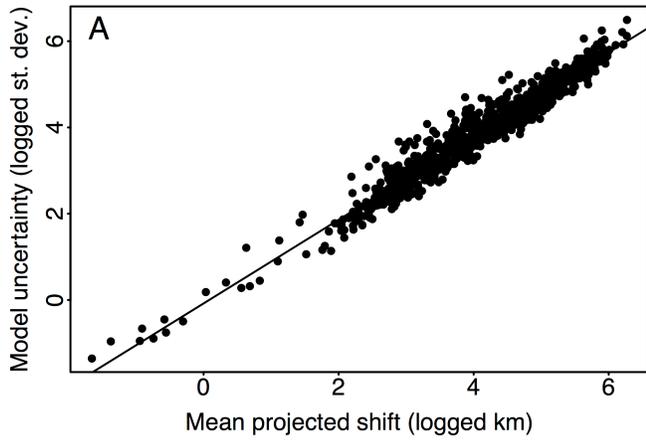
- 941 47. Folk RL. Petrology of Sedimentary Rocks. Austin, TX: Hemphill Publishing; 1980.
- 942 48. NOAA and DoD. U.S. Chart No. 1: Symbols, Abbreviations and Terms Used on Paper
- 943 and Electronic Navigational Charts; 2013.
- 944 49. Reid JM, Reid JA, Jenkins CJ, Hastings ME, Williams SJ, Poppe LJ. usSEABED:
- 945 Atlantic coast offshore surficial sediment data release. U.S. Geological Survey Data
- 946 Series 118; 2005. <http://pubs.usgs.gov/ds/2005/118/>.
- 947 50. Buczkowski BJ, Reid JA, Jenkins CJ, Reid JM, Williams SJ, Flocks JG. usSEASBED:L
- 948 Gulf of Mexico and Caribbean (Puerto Rico and U.S. Virgin Islands) offshore surficial
- 949 sediment data release. U.S. Geological Survey Data Series 146; 2006.
- 950 <http://pubs.usgs.gov/ds/2006/146/>.
- 951 51. Reid JA, Reid JM, Jenkins CJ, Zimmermann M, Williams SJ, Field ME. usSEABED:
- 952 Pacific Coast (California, Oregon, Washington) offshore surficial-sediment data release.
- 953 U.S. Geological Survey Data Series 182; 2006. <http://pubs.usgs.gov/ds/2006/182/>.
- 954 52. Pebesma EJ. Multivariable geostatistics in S: the gstat package. Computers &
- 955 Geosciences. 2004; 30:683-691.
- 956 53. Graler B, Pebesma E, Heuvelink G. Spatio-Temporal interpolation using gstat. The R
- 957 journal. 2016; 8(1): 204-218.
- 958 54. Loring DH, Nota DJG. Morphology and sediments of the Gulf of St. Lawrence. Bull Fish
- 959 Res Board Canada. 1973; 182.
- 960 55. Wood SN. Fast stable restricted maximum likelihood and marginal likelihood estimation
- 961 of semiparametric generalized linear models. J Roy Stat Soc B. 2011; 73(1): 3-36.
- 962 56. Wood SN. Generalized additive models: an introduction with R. Chapman & Hall/CRC.
- 963 Florida. 2006; 410p.
- 964 57. Maunder MN, Punt AE. Standardizing catch and effort data: a review of recent
- 965 approaches. Fisher Res. 2004; 70:141-159.
- 966 58. Bacheler N, Shertzer K, Reichert M, Stephen J, Pate M. Standardized CPUE of black sea
- 967 bass (*Centropristis striata*) caught in blackfish and Florida snapper traps deployed by
- 968 MARMAP. SEDAR25-DW02. 2011; 19p. <http://sedarweb.org>
- 969 59. Thorson JT, Ward EJ. Accounting for vessel effects when standardizing catch rates from
- 970 cooperative surveys. Fisher Res. 2014; 155:168-176.
- 971 60. Hijmans RJ, Phillips S, Leathwick J, Elith J. dismo: species distribution modeling. R
- 972 package version 1.1-4. 2017. <https://CRAN.R-project.org/package=dismo>.
- 973 61. Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, et al. Novel methods
- 974 improve prediction of species' distributions from occurrence data. Ecography (Cop.).
- 975 2006; 29:129–151.
- 976 62. Taylor KE, Stouffer RJ, Meehl GA. An overview of CMIP5 and the experimental design.
- 977 Amer Meteor Soc. 2012; 485-498.
- 978 63. Hijmans RJ. geosphere: spherical trigonometry. R package version 1.5-5. 2016.
- 979 <http://CRAN.R-project.org/package=geosphere>.
- 980 64. Koenker R. quantreg: quantile regression. R package version 5.33. 2017.
- 981 <https://CRAN.R-project.org/package=quantreg>.
- 982 65. Portner HO, Knust R. Climate change affects marine fishes through the oxygen limitation
- 983 of thermal tolerance. Science. 2007; 315:95-97.
- 984 66. Deutsch C, Ferrel A, Seibel B, Portner H-O, Huey RB. Climate change tightens a
- 985 metabolic constraint on marine habitats. Science. 2015; 348:1132-1135.

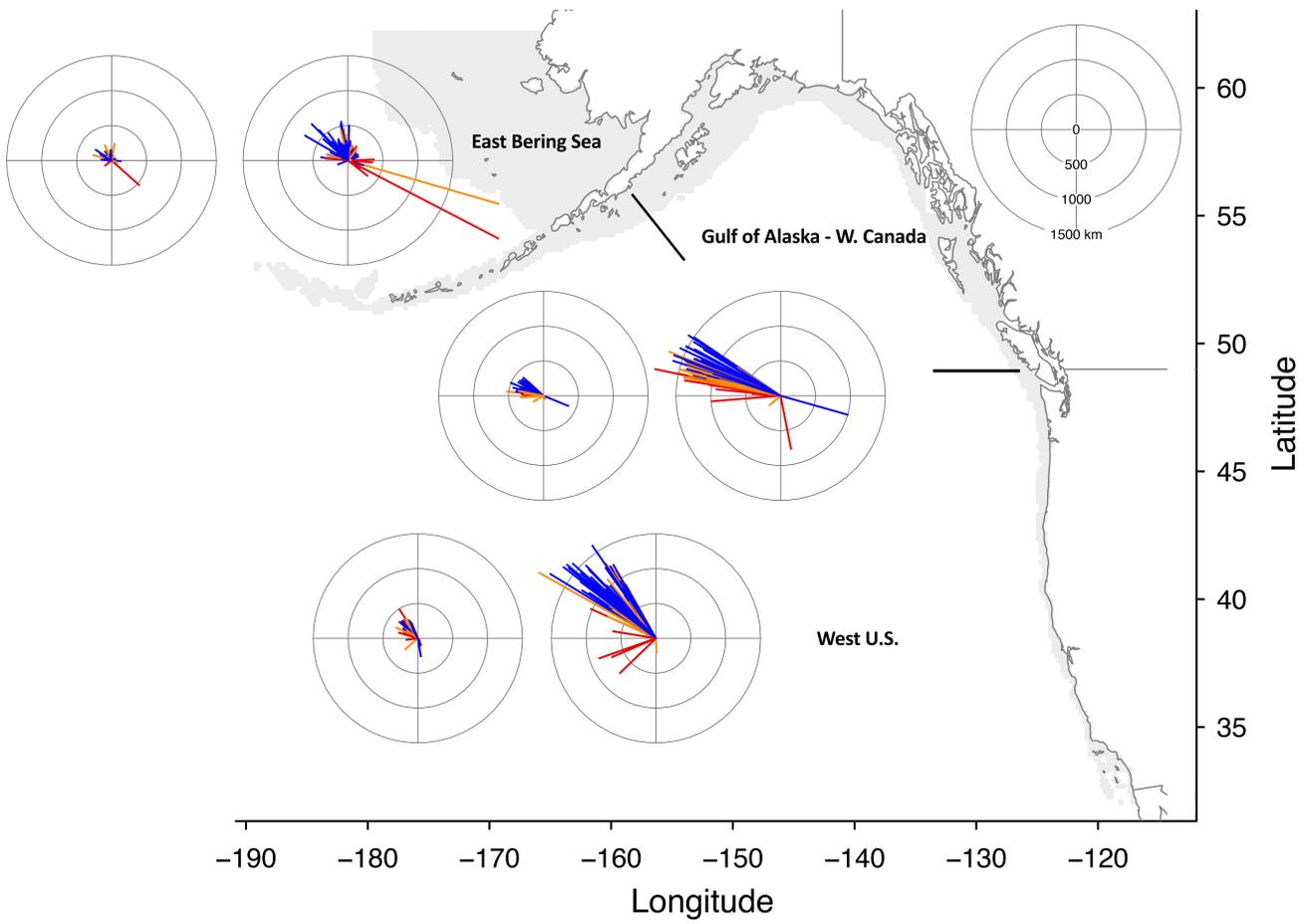
- 986 67. Jones MC, Cheung WWL. Multi-model ensemble projections of climate change effects  
987 on global marine biodiversity. *ICES J Mar Sci.* 2015; 72:741-752.
- 988 68. Sunday JM, Pecl GT, Frusher S, Hobday AJ, Hill N, Holbrook NJ, et al. Species traits  
989 and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol*  
990 *lett.* 2015; 18:944-953.
- 991 69. Bopp L, Resplandy L, Orr JC, Doney SC, Dunne JP, Gehlen M, Halloran P, et al.  
992 Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5  
993 models. *Biogeosciences.* 2013; 10:6225-6245.
- 994 70. Burrows MT, Schoeman DS, Richardson AJ, Molinos JG, Hoffmann A, Buckley LB, et  
995 al. Geographical limits to species-range shifts are suggested by climate velocity. *Nature.*  
996 2014; 507:492-495.
- 997 71. Fossheim M, Primicerio R, Johannessen E, Ingvaldsen RB, Aschan MM, Dolgov AV.  
998 Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat*  
999 *Clim Chang.* 2015; 5:673-677.
- 1000 72. Wisz MS, Broennimann O, Gronkjaer P, Moller PR, Olsen SM, Swingedouw D, et al.  
1001 Arctic warming will promote Atlantic-Pacific fish interchange. *Nat Clim Chan.* 2015;  
1002 5:261-265.
- 1003 73. Wuenschel MJ, Hare JA, Kimball ME, Able KW. Evaluating juvenile thermal tolerance  
1004 as a constraint on adult range of gray snapper (*Lutjanus griseus*): a combined laboratory,  
1005 field and modeling approach. *J Exp Mar Biol Ecol.* 2012; 436-437:19-27.
- 1006 74. Rykaczewski RR, Dunne JP, Sydeman J, Garcia-Reyes M, Black BA, Bograd SJ.  
1007 Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern  
1008 boundary currents through the 21st century. *Geophys Res Lett.* 2015; 42:6424-6431.
- 1009 75. Brady RX, Alexander MA, Lovenduski NS, Rykaczewski RR. Emergent anthropogenic  
1010 trends in California Current upwelling. *Geophys Res Lett.* 2017; 44:5044-5052.
- 1011 76. Jones MC, Dye SR, Pinnegar JK, Warren R, Cheung WWL. Using scenarios to project  
1012 the changing profitability of fisheries under climate change. *Fish Fisher.* 2015; 16:603-  
1013 622.
- 1014 77. Dormann CF. Effects of incorporating spatial autocorrelation into the analysis of species  
1015 distribution data. *Glob Ecol Biogeogr.* 2007; 16:129-138.
- 1016 78. Rijnsdorp AD, Peck MA, Engelhard GH, Mollmann C, Pinnegar JK. Resolving the effect  
1017 of climate change on fish populations. *ICES J Mar Sci.* 2009; 66:1570-83.
- 1018 79. Cheung WWL, Reygondeau G, Frolicher TL. Large benefits to marine fisheries of  
1019 meeting the 1.5°C global warming target. *Science.* 2016; 354:1591-1594.
- 1020 80. Pinsky ML, Fogarty M. Lagged social-ecological responses to climate and range shifts in  
1021 fisheries. *Clim chang.* 2012; 115:883-891.
- 1022 81. Link JS, Nye JA, Hare JA. Guidelines for incorporating fish distribution shifts into a  
1023 fisheries management context. *Fish Fisher.* 2011; 12:461-469.
- 1024 82. Pinsky ML, Mantua NJ. Emerging adaptation approaches for climate-ready fisheries  
1025 management. *Oceanography.* 2014; 27(4):146-159.
- 1026 83. Colburn LL, Jepson M, Weng C, Seara T, Weiss J, Hare JA. Indicators of climate change  
1027 and social vulnerability in fishing dependent communities along the eastern and gulf  
1028 coasts of the United States. *Mar Pol.* 2016; 74:323-333.
- 1029  
1030  
1031

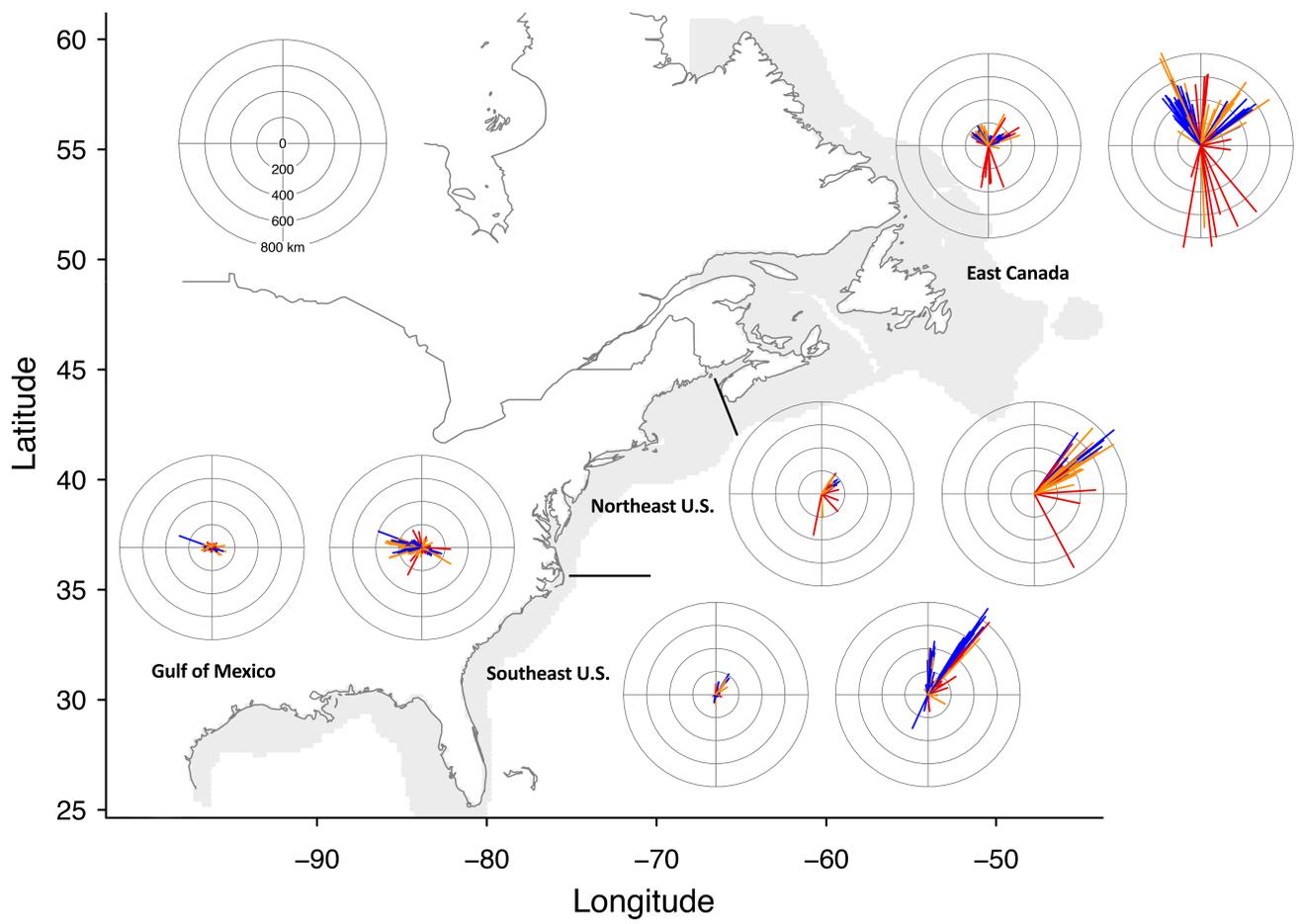
1032 **Supporting information**

1033 **S1 Appendix. List of projected species.** The proportion of deviance explained for each GAM  
1034 habitat model (presence-absence and biomass) along with the geographic region used to group  
1035 each species, the level of projection uncertainty, and the mean and standard deviation of  
1036 projections in both distance shifted (km) and change in habitat availability (%) over the course of  
1037 the 21<sup>st</sup> century for both RCP 2.6 and 8.5.

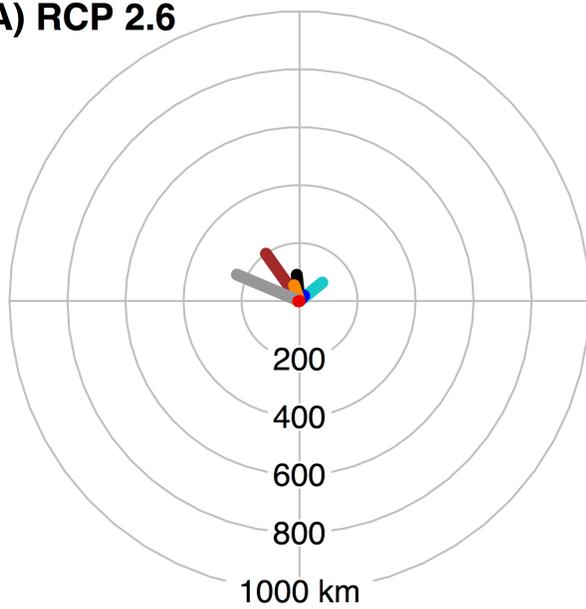




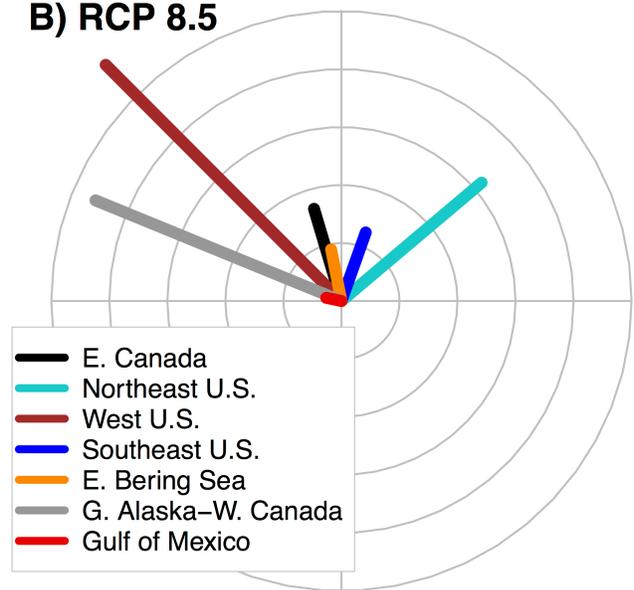




**A) RCP 2.6**



**B) RCP 8.5**



- E. Canada
- Northeast U.S.
- West U.S.
- Southeast U.S.
- E. Bering Sea
- G. Alaska-W. Canada
- Gulf of Mexico

