

Projecting marine fish distributions during early life stages under future climate scenarios

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Authors: Rebecca A. Howard¹, Lauren A. Rogers², Kelly A. Kearney³, Laura L. Vary¹, Lorenzo Ciannelli¹

Correspondence Contact Information:

Rebecca A. Howard

Email: howardre@oregonstate.edu

Affiliations:

¹*College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA*

²*Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, USA*

³*Cooperative Institute for Climate, Ocean, and Ecosystem Studies, University of Washington, Seattle, WA, USA*

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Abstract

Changes to Earth's climate affect organisms globally; in marine systems these impacts are seen through warming water temperatures, ocean acidification, hypoxia, and frequent marine heatwaves. These effects may lead to movement of species to more favorable conditions. While climate-driven movement is well studied at the adult stage, how early life stages of marine fish will respond to future variability is less clear. Many fish species are constrained by specific spawning locations or phenology. Spawning in certain locations allows for local retention of offspring while precise timing can facilitate transport of offspring to nursery locations through seasonal circulation patterns. Our research investigates how changing oceans impact the location and timing of spawning of Bering Sea groundfishes over the next century. We used ROMS SST and SSS model output and NOAA survey data in species distribution models to hindcast and project distributions and center of gravity for eggs and larvae of six groundfish species. Our analyses found that most of our study species exhibit flexible geography. However, the speed and direction of egg and larval movement did not track the speed and direction of their respective thermal niches. Hence, projected distributional patterns of adult stages may be limited by their early life stages. This response is likely to be mirrored globally by other species with planktonic eggs and larvae. These results indicate that life history considerations are critical for management of commercially important species, as effects on early life stages are strongly connected to the success or failure of adult populations.

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1 **1 Introduction**

2 Climate change resulting from rising atmospheric carbon dioxide and subsequent increases in
3 global temperature has been documented to have significant physical and biological impacts on
4 marine ecosystems (Bindoff et al., 2019; Bograd et al., 2023; Poloczanska et al., 2016). Specific
5 impacts on ocean conditions include rising ocean temperatures in the Northeast Atlantic (Belkin,
6 2009), as well as extreme events like marine heatwaves in the North Pacific (Litzow et al., 2024).
7 Climate change may also be connected to the recent warming observed along the west coast of
8 Australia (Wernberg et al., 2013) and record low winter sea ice extent in the Bering Sea region in
9 2018 and 2019 (Stabeno & Bell, 2019). Physical oceanographic changes like these have
10 ecological implications such as reductions in suitable habitat for certain species (Lynch et al.,
11 2015; Morato et al., 2020), mass die-offs (Szuwalski et al., 2023), and the spatial expansion or
12 contraction of community assemblages (Kleisner et al., 2016). These effects on marine biota are
13 expected to continue and thus will impact coastal communities that depend on these systems
14 (Rogers et al., 2019). It is therefore imperative to understand more thoroughly how species
15 respond to changes in their environment, allowing for insight into the biological consequences of
16 a changing ocean.

17

18 It is well established that the environment in which egg production and larval fish development
19 occurs strongly affects the survival of the early life stages and, subsequently, the adult population
20 (Cushing, 1975, 1990; Hjort, 1914). Beginning with Hjort's (1914) critical period hypothesis,
21 early life history research has continued to provide important insights into these vulnerable
22 stages. For example, small fluctuations in temperature are known to reduce egg survival and
23 development (Blaxter, 1991). At higher temperatures, larval metabolic, developmental, and

24 growth rates are enhanced (Blaxter, 1991; Houde, 1989; Pepin, 1991) but time spent in the water
25 column and during metamorphosis are reduced (O'Connor et al., 2007; Sponaugle et al., 2006).
26 The effects of temperature on eggs and larvae impose a constraint, potentially explaining why
27 spawning adults evolve to reproduce in specific locations and at certain times. There are
28 additional evolutionary constraints on fish spawning habitats, linked to the developmental phases
29 of the embryo, species' social structure, and reproductive ecology of spawning adults (Ciannelli
30 et al., 2015). However, it is unclear how those constraints will be affected in the future as ocean
31 conditions change and areas previously suitable for spawning become less optimal for eggs and
32 larvae (Pankhurst & Munday, 2011). Understanding how early life stages will respond to climate
33 change expands upon and enhances previous research focused on adult stages, providing a better
34 foundation for managers and policymakers to anticipate impacts on commercial fisheries.

35
36 Predicting future distributions of marine species under different climate change scenarios is
37 possible with use of large-scale climate projections and can provide general insight into how
38 species may be affected (Cheung et al., 2009; Pinsky et al., 2020). Species distribution models
39 (SDMs) are a statistical tool commonly used to create long-term projections for terrestrial,
40 freshwater, and marine species. In marine long-term models, climate projections are often used
41 with fishery survey data to predict how species will generally respond to environmental change,
42 whether fishing grounds may shift, and which species are most likely to survive over the next
43 century (Cote et al., 2021; Moltó et al., 2021). Marine SDMs have primarily focused on adult
44 stages and in only a few instances have models been developed to project future larval
45 distributions (Muhling et al., 2020) and suitable spawning habitat (Bigman et al., 2023;
46 Erauskin-Extramiana et al., 2019; Lima et al., 2022; Maynou et al., 2020; Sandø et al., 2020).

47 Developing projections of spawning distributions and early life stages therefore have the
48 potential to provide additional information about how the most critical point in the fish life cycle
49 may be affected by climate change. While data on adults are more abundant than that for early
50 life stages, long time series of egg and larval data are available in regions such as the Bering Sea,
51 thus providing an opportunity to fill this research gap.

52

53 Some of the world's most productive commercial fishing grounds are found in the Bering Sea
54 (Figure 1), including the largest fishery in North America: walleye pollock (*Gadus*
55 *chalcogrammus*). It is also the location of a 30+ year time-series of biennial scientific surveys
56 targeting fish early life stages. Understanding how the eggs and larvae of commercially
57 important species of the Bering Sea will be affected by climate change is crucial for the
58 sustainability of the region's fisheries and will provide insight into potential applications of
59 similar methods to other regions and species. Distributions of early life stages are often used to
60 study spawning location and timing (Bacheler et al., 2010; Rogers & Dougherty, 2019), and
61 cumulatively reflect the contributions of both spawning output and early life stage survival
62 processes. Understanding changes in spawning distributions can provide insight into whether the
63 offspring of marine species will continue to be retained in suitable nursery habitat or have access
64 to specific currents needed to transport them to favorable locations. In this study, we investigate
65 how changing oceanographic conditions have historically, and may in the future, impact the
66 location and timing of spawning of Bering Sea groundfishes. Here, we use early life stages of
67 groundfishes as a proxy for spawning location and timing. We examine whether species are more
68 likely to be flexible in their location or timing of spawning, whether egg and larval centers of
69 gravity (COG) follow similar trajectories, and how these species track climate velocity.

70 Evaluation of COG and climate velocity were conducted to determine whether separation
71 between life stages will occur due to climate change and if these species are likely to adapt to
72 warming waters by shifting at the speed of their thermal niche. We expected to see differences in
73 types of flexibility between species with different life histories but similarities in trajectory and
74 climate velocity tracking between eggs and larvae of the same species.

75

76 **2 Materials & Methods**

77 **2.1 Biological data**

78 Ichthyoplankton data for six species were obtained from the NOAA Alaska Fisheries Science
79 Center's (AFSC) and Pacific Marine Environmental Lab's joint research program: the
80 Ecosystems and Fisheries-Oceanography Coordinated Investigations (EcoFOCI) Bering Sea
81 surveys. Data used for this research were collected between 1988 – 2017 from February to early
82 October using a fixed station grid, though sampling is primarily between April and June. The
83 surveys conducted by EcoFOCI use oblique tows to depths 5 m from the seafloor with 60-cm
84 diameter bongo nets with 333 or 505 μm mesh to capture fish eggs and larvae. Difference in
85 mesh size has not been found to affect ichthyoplankton catch rates for this survey (Boeing &
86 Duffy-Anderson, 2008; Shima & Bailey, 1994). The volume of water filtered was measured by a
87 flowmeter mounted at the opening of each net. Ichthyoplankton preserved at sea in formalin
88 were identified to species at the Plankton Sorting and Identification Center in Szczecin, Poland.
89 Taxonomic verifications were conducted by the EcoFOCI Program. Catch per unit effort (CPUE)
90 at each station for each species was calculated as count of larvae or eggs per 10 m^2 .

91

92 The six species selected for the present analyses are all commercially important fishes abundant
93 in the survey time series and exhibit differing life history strategies. Four Pleuronectids (flatfish)
94 were selected: Alaska plaice (*Pleuronectes quadrituberculatus*), yellowfin sole (*Limanda*
95 *aspera*), northern rock sole (*Lepidopsetta polyxystra*), and flathead sole (*Hippoglossoides*
96 *elassodon*). Two species of Gadid, Pacific cod (*Gadus macrocephalus*) and walleye pollock
97 (hereafter, “pollock”), were also chosen. Sufficient egg data were only available for pollock,
98 flathead sole, and Alaska plaice, as both northern rock sole and Pacific cod produce demersal
99 eggs while yellowfin sole eggs were not captured in significant quantities. Larval data were
100 available for all six species. For each species, the ichthyoplankton data were trimmed to ensure
101 our analysis focused on the habitat of the species during the time of year eggs and larvae are
102 present. Stations further than 30 km from an observation of the species were removed from the
103 final prediction dataset, as were data collected in months during which few eggs or larvae were
104 collected.

105

106 **2.2 Environmental data**

107 The explanatory variables in the models included temperature (°C) and salinity. These covariates
108 were obtained from a reanalysis-forced hindcast simulation of the Bering10K model, a Bering
109 Sea implementation of the Regional Ocean Modeling System (ROMS). This model has
110 demonstrated skill in reproducing the thermal environment of the Bering Sea shelf; see Kearney
111 et al. (2020) and citations within for a full description, history, and validation of this regional
112 model and the hindcast simulations. The Bering10K model has a 10 km horizontal grid
113 resolution with 30 vertical layers. The Bering10K model was also used to dynamically
114 downscale six simulations from Phase 6 of the Coupled Model Intercomparison Project (CMIP6;

115 O'Neill et al., 2016). Three Earth System Models (ESM) and two emission scenarios were used.
116 The ESMs were chosen to span the range of projections within the full CMIP6 suite, choosing
117 models with high, low, and near-median thermal sensitivities. These include the CESM version 2
118 with Community Atmospheric Model version 6 (Danabasoglu et al., 2020), GFDL Earth System
119 Model version 4.1 (Dunne et al., 2020), and the MIROC Earth System version 2 for long-term
120 simulations. These will hereafter be referred to as CESM, GFDL, and MIROC. The emission
121 scenarios used are two of the Shared Socio-economic Pathways (SSPs) - a low carbon mitigation
122 scenario, SSP5-8.5, and a high carbon mitigation scenario, SSP1-2.6 - which describe possible
123 combinations of future mitigation and adaptation challenges that lead to different levels of
124 radiative forcing (Riahi et al., 2017).

125
126 Temperature and salinity from the model's top layer, or surface, provided model-generated co-
127 located values of sea surface temperature (SST) and sea surface salinity (SSS). Hindcasted SST
128 and SSS values for specific locations were matched to the nearest EcoFOCI survey station using
129 nearest neighbor search through the 'nn2' function in the *RANN* R package (Arya et al., 2019).
130 Downscaled projections of SST and SSS for each ESM-forced model and SSP were bias
131 corrected using the delta method, as described in Holsman et al. (2020). This bias correction
132 method compares each ESM and the hindcast during a reference period to correct for differences
133 in time-series means and variances. In doing so, SDMs parameterized with hindcast output can
134 provide more realistic future predictions of fish spatial distributions when applied to the bias
135 corrected projections compared to the raw projections. The equation used here is as follows:

136
137
$$T'_{fut,y} = \bar{T}_{hind,ref} + \frac{\sigma_{hind,ref}}{\sigma_{fut,ref}} (T_{fut,y} - \bar{T}_{fut,ref}) \quad (1)$$

138

139 where $T'_{fut,y}$ provides the adjusted projected SST or SSS values while $T_{fut,y}$ represents the
140 original projected values and $\bar{T}_{fut,\overline{ref}}$ represents a projected mean for the reference years, which
141 is derived from the historical period. $\bar{T}_{hind,ref}$ represents the reference year period hindcast mean
142 while σ refers to the standard deviation during the reference period for either the hindcast or
143 projections. A reference period of 1980 – 2014 and projected SST and SSS from 2015 – 2099 for
144 each SSP and ESM combination were used. Both SSPs and all ESMs indicate a trend in
145 increasing temperature over the next century (Figure 2).

146

147 **2.3 Model parameterization**

148 Generalized additive models (GAM), a type of regression model that can capture nonlinear
149 relationships, were used to estimate the abundance of fish eggs and larvae as a function of
150 environmental variables. Models were first parameterized using hindcasts in order to determine
151 the best model for each species and life stage. The best model was then used to predict future
152 fish distributions using Bering10K-derived projections of SST and SSS.

153

154 Multiple GAM formulations were evaluated and models using a Tweedie response distribution
155 were ultimately selected due to the zero-inflated nature of the egg and larval data. The Tweedie
156 distribution is a form of a compound Poisson-gamma distribution due to the use of a power
157 parameter, estimated in this case through the ‘tw’ function in the *mgcv* R package (Tweedie,
158 1984; Wood, 2017). Use of a Tweedie distribution allowed for better handling of an abundance
159 of zeroes in these data, which is common in fisheries data (Shono, 2008). To determine the best
160 model, several formulations were compared. These included a base model with only spatial and

161 temporal covariates and a set of additional models with progressively more complex
162 specifications of environmental covariates. The base model formulation included only latitude
163 and longitude (ϕ, λ) as a tensor product and day of the year (J) as nonparametric thin plate
164 splines (s). Latitude and longitude were included due to the ability of spatial covariates to
165 improve SDM projections for organisms that are not highly mobile, such as eggs and larvae
166 (Brodie et al., 2022). Day of the year was included as a way to correct for possible effects of the
167 differences in timing of survey across years and to characterize the phenology of egg or larval
168 production. Year (y) was included as a random effect in order to allow removal when projecting.
169 A log-link (g) provided the link between CPUE and each predictor. This model is described as
170 follows:

171

$$172 \quad g(\text{CPUE}) = re(y) + te(\phi, \lambda) + s(J) \quad (2)$$

173

174 Varying coefficient terms were incorporated into additional models to allow for increased
175 flexibility in spawning location or timing (Bacheler et al., 2012; Hastie et al., 2001). In this case,
176 location and timing were allowed to vary linearly with temperature, which was a mean index
177 value for each year. The mean temperature index (T) was calculated using SST values from
178 February 1 to April 30 for each year for an area over the continental shelf with dimensions of
179 latitude 56°N to 58°N and longitude -165°W to -170°W . This area was chosen to provide an
180 annual index of cold and warm years over the Bering Sea continental shelf. Thus, the time frame
181 and spatial dimensions for T remained the same for each species. Collocated SST, SSS, and the
182 varying coefficient terms were included as thin plate splines for each independent variable. The
183 two equations used are as follows:

184

$$185 \quad g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(\phi, \lambda, by = T) \quad (3)$$

186

$$187 \quad g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(J, by = T) \quad (4)$$

188

189 Equation 3 allows for the effect of location to vary as a function of the temperature index while
190 Equation 4 allows for the effect of time to vary as a function of the temperature index. For each
191 model, the maximum number of knots were specified as five for the SST and SSS splines and as
192 nine for the day of the year. Day of the year was allowed to have a higher number of knots to
193 characterize the potential multiple spawning peaks. To prevent inappropriate extrapolation in the
194 projection beyond the covariate ranges existing in the hindcast, each term was penalized based
195 on their first derivative (Barnes et al., 2022). We used Akaike's information criterion (AIC) to
196 select the best model for each species and life stage (Akaike, 1974). The base models and
197 varying coefficient models were also compared to models that included the splines for SST and
198 SSS, but excluded the varying coefficient term (Table S1). To further evaluate the benefit of
199 including varying coefficient terms, overall model mean square error (MSE) was calculated for
200 all models and percent reduction in MSE compared to the base model was calculated. In each
201 case, MSE was reduced for the models containing a varying coefficient term and the same model
202 was selected as through AIC, with the exception of flathead sole larvae (Table S2).

203

204 **2.4 Distribution projections**

205 Once model parameterization was complete, the final models were used to project future
206 distributions of eggs and larvae in the Bering Sea. The projection period was divided into three

207 time periods: early (2015-2039), middle (2040-2069), and late century (2070-2099). For each
208 year within a period, a prediction grid of latitudes and longitudes with approximately a 10 km
209 resolution covering the study region, similar to the ROMS grid, was generated using a month and
210 day of year that corresponded approximately to the peak of abundance of fish larvae and/or eggs
211 for each species. At this point, the grids for each year were identical for each species and stage
212 combination. Then, monthly SST and SSS values from the top layer of each year of the ROMS
213 projection model output was matched to the nearest location on a given year's prediction grid
214 using the 'nn2' function in the *RANN* package in R (Arya et al., 2019). The temperature index
215 was also calculated for each year within the period for use in the varying coefficient term. Year,
216 which was included as a random effect during model parameterization, was excluded from the
217 projection models. Predictions of egg and larval abundance for each period were scaled from
218 zero to one based on minimum and maximum values of abundance each year to allow for
219 comparison between time periods and to focus only on changes in distribution.

220
221 Center of gravity (COG) for each species and stage along with thermal niche were calculated to
222 assess potential connectivity changes over time between life stages and determine if these
223 species are overall projected to track suitable thermal conditions. COG in latitude and longitude
224 (ϕ, λ) units was calculated for the scaled predictions (S) for each year within each time period,
225 then averaged across the time period. Latitude and longitude were calculated separately using the
226 following:

227
228
$$COG_{\phi} = \frac{\sum_i^n \phi_i \cdot S_i}{\sum_i^n S_i} , \quad COG_{\lambda} = \frac{\sum_i^n \lambda_i \cdot S_i}{\sum_i^n S_i} \quad (5)$$

229

230 The same prediction grid spatial dimensions were used for all species, stages, time periods, and
231 scenarios to allow for comparison. As with the hindcast prediction grid, cells more than 30 km
232 from a positive sample in the survey data were removed for all grids. The haversine distance
233 (km) between COG of eggs and larvae of the same species was calculated for each time period.

234

235 Thermal COG for SST was calculated using a similar formula to Equation 5. SST values were
236 determined to be inside or outside the thermal range of a given species using the 95% confidence
237 interval of the SST partial dependence curves generated by the species' final parameterized
238 model. Values with significant positive effects on abundance for a given species and stage were
239 assigned a value of one and all others assigned zero. Thermal COG in latitude and longitude
240 units was calculated separately for each species grid. Using the assigned values (A), thermal
241 COG was calculated for each year as follows:

242

$$243 \quad COG_{\phi} = \frac{\sum_i^n \phi_i A_i}{\sum_i^n A_i} \quad , \quad COG_{\lambda} = \frac{\sum_i^n \lambda_i A_i}{\sum_i^n A_i} \quad (6)$$

244

245 To determine if species track thermal habitat, rate of change per year in COG location was
246 calculated for both species distribution and thermal COG. Following the methods of Pinsky et al.
247 (2013), latitude was regressed against year to calculate the slope, or rate of change, for each time
248 period. The sign of slope values indicate the direction of movement of COG during a given time
249 period, with negative rates indicating southward movement and positive rates indicating
250 northward movement. Then, to evaluate if species distribution COGs (S) are expected to track
251 thermal COGs (T), bias was calculated as follows for each species and time period (t):

252

253 $B_t = \text{sign}(\text{COG}_{\phi,T,t}) \times (\text{COG}_{\phi,S,t} - \text{COG}_{\phi,T,t})$ (7)

254

255 Positive biases indicate that a species tracks thermal COG, while negative biases indicate a lag or
256 potential movement away from thermal COG. A t-test of bias for all species and stages was used
257 to determine if species distribution COGs lag thermal COG for each time period. All analyses
258 described above are publicly available (Howard, 2024).

259

260 **3 Results**

261 **3.1 Hindcast**

262 All models selected during parameterization with the hindcast output included a varying
263 coefficient term (Table S1). For all species except Pacific cod, the best fit model included the
264 location varying coefficient (Equation 3; Tables 1, S2). The model with the time varying
265 coefficient was the best fit for Pacific cod larvae.

266

267 Temporal and spatial patterns in abundance throughout the survey period varied by species and
268 life stage, illustrating phenological differences across species, as well as how different life stages
269 may be affected by the mean temperature index (Figure 3). In general, seasonal peaks in larval
270 abundance followed periods of high egg abundance for the species for which both stages were
271 available. There were very clear peaks in abundance at different points in the year for pollock
272 eggs (March), flathead sole eggs (May), and Alaska plaice larvae (June). Multiple peaks in
273 abundance throughout the year were apparent for flathead sole larvae (May and July), yellowfin
274 sole (July and September), Pacific cod (April and June), and northern rock sole (April, June, and
275 August). Pollock larvae and Alaska plaice eggs had peaks in abundance at the beginning and end

276 of the sampled period, respectively, and thus their full temporal distribution each year was not
277 well sampled.

278

279 In terms of phenology, for most species an increase in the mean temperature index led to
280 increases in abundance throughout the sampled period (Figure 3). In many cases, these
281 directional shifts in abundance were most apparent during seasonal periods in which abundance
282 peaks. For example, for Alaska plaice eggs, there was a decrease in abundance with a 1°C
283 increase in temperature at the beginning of the seasonal series. In contrast, an increase in
284 temperature led to increased abundance at some phenological peaks or high points for larvae of
285 pollock, Alaska plaice, flathead sole, and yellowfin sole. Effects of mean temperature on
286 phenology were mixed for Pacific cod and northern rock sole larvae while there was no change
287 for pollock and flathead sole eggs. For Pacific cod, warmer temperatures resulted in contraction
288 of the larval period. A clear peak in Pacific cod abundance was apparent near the middle of the
289 season with a 1°C increase in temperature but decreases or no change were seen during other
290 times of the year. Spatially, positive effects of a 1°C increase in temperature on abundance were
291 clear for larvae of pollock, flathead sole, Alaska plaice, yellowfin sole, and Pacific cod. Negative
292 effects were apparent for pollock eggs and northern rock sole, though positive effects on
293 abundance were found in some areas. Spatial effects were mixed for flathead sole and Alaska
294 plaice eggs. In general, egg abundance seemed more likely to decrease with increases in mean
295 shelf temperature while larval abundance typically increased, though maps of change indicate
296 effects of temperature may be location dependent.

297

298 Relationships with SST and SSS were variable depending on species and life stage, though the
299 lowest temperatures were often associated with negative effects on abundance (Figure 3). Partial
300 dependence plots showed either peaks where temperature had a positive effect on abundance,
301 like for Alaska plaice larvae, or one clear transition from negative to positive effects on
302 abundance, like flathead sole larvae. SSS relationships with abundance were also variable. Some
303 species stages, like pollock larvae and flathead sole eggs, exhibited little change over the full
304 range of salinity values. For others, like Alaska plaice larvae, lower salinities were related to
305 positive effects on abundance, while conversely, for species such as northern rock sole larvae,
306 higher salinities were found to correlate with higher abundance.

307

308 Maps of the location varying coefficient term (Figures 4, S1-S4) illustrated the spatial effects of
309 mean temperature on abundance for all species except Pacific cod, for which the time varying
310 coefficient term was selected, with positive effects primarily on the inner shelf and negative
311 effects located along the Alaska Peninsula for most species. Nonetheless, effects of the varying
312 coefficient term were different for each species and stage. For example, pollock egg and larval
313 maps showed positive effects of increases in temperature on abundance over the northeastern
314 continental shelf, near Unimak Pass, and northeast of Unalaska (Figure 4). Negative effects on
315 pollock abundance as a result of increased temperature were found along the Alaska Peninsula
316 and southeast of the Pribilof Islands. There were additional negative effects on the abundance of
317 pollock eggs to the southeast of the Pribilof Islands. Flathead sole varying coefficient maps
318 showed clear differences between stages, with both negative and positive effects on egg
319 abundances (Figure S1). For example, negative effects of increases in temperature on egg
320 abundances were evident along the Alaska Peninsula and east of the Pribilof Islands. Positive

321 effects for flathead sole eggs were found to be concentrated in the middle of the study region but
322 for larvae they were dispersed across the shelf. In contrast to other species, direction of
323 temperature effects for Alaska plaice were generally specific to stage: negative effects were
324 primarily seen for eggs whereas positive effects were seen for larvae (Figure S2). Yellowfin sole
325 exhibited mainly positive effects from increases in temperature, particularly in the southeast
326 along the Alaska Peninsula (Figure S3). Northern rock sole positive effects were greatest near
327 Unalaska Island and between 56 and 58°N on the inner shelf, while negative effects were
328 dispersed across the outer shelf and along the inner Alaska Peninsula (Figure S4). Location
329 varying coefficient maps for Pacific cod were not created as the best fit model was that
330 containing the time varying coefficient term (Table 1, S2).

331

332 **3.2 Projections**

333 The projected distributions for each stage and species showed varied responses to changes in
334 temperature and salinity over the next century, both in terms of overall spatial patterns and
335 trajectories of each COG. Pollock eggs, for example, were predicted to be concentrated around
336 the Pribilof Islands at the beginning of the century (2015-2039) but by the end (2070-2099) were
337 dispersed across the continental shelf and were expected to become more concentrated near
338 Unimak Pass in the future (Figure 5). Pollock larvae, in contrast, appeared to have a less
339 noticeable change in spatial patterns and areas of high abundance remained consistent over time,
340 albeit with decreases in abundance. When comparing emission scenarios, pollock egg and larval
341 abundances appeared to be higher throughout the region for the high emission scenario by the
342 end of the century. Little change in distributional pattern over time was observed for flathead
343 sole eggs, which appeared to further concentrate at 56°N (Figure S5). Flathead sole larvae also

344 became more concentrated in a smaller area by the end of the century, but were instead predicted
345 to be located at 58°N. These effects were seen for both emission scenarios. Alaska plaice eggs
346 and larvae were predicted to be distributed on the shelf near the boundary of the study area,
347 centered at about 60°N (Figure S6). In both cases, the distributions became more concentrated at
348 the northern edge of the study area over the next century, possibly indicating movement into the
349 Northern Bering Sea. For larvae, the high abundance near the Alaska Peninsula all but
350 disappeared by the end of the century. Yellowfin sole larvae were located along much of the
351 inner shelf at the beginning of the century but were predicted to become highly concentrated in
352 Bristol Bay by the end of the century (Figure S7). Northern rock sole larvae became more
353 concentrated at 56°N above the Alaska Peninsula by the end of the century, though an area of
354 high abundance remained in Unimak Pass (Figure S8). Pacific cod larvae distributions changed
355 very little over the three time periods, with the highest abundances also remaining through
356 Unimak Pass and around Unimak Island (Figure S9). For yellowfin sole, northern rock sole, and
357 Pacific cod, differences between the two emission scenarios were not apparent.

358

359 Movement of species distribution COG over the next century was evaluated for all species and
360 distance between life stage COG was compared for pollock, flathead sole, and Alaska plaice.
361 Pollock, flathead sole, and Alaska plaice were the three species for which predicted average
362 COG trajectory over the next century was northward (Table 2, Figure 6). Yellowfin sole
363 movement was predicted to be southward, while northern rock sole were expected to move east
364 and Pacific cod to move west. The COGs for the eggs and larvae of pollock and Alaska plaice
365 moved closer together by the end of the century, which was in contrast to flathead sole for which
366 the COGs moved slightly further apart (Table S3). While the average direction of movement for

367 pollock and Alaska plaice life stage COGs differed slightly, the reduced distance between each
368 COG by the end of the century may indicate more overlap of the life stages of these species.

369

370 By evaluating thermal COG, we found that thermal habitat of all species and life stages moved
371 northward despite only half of the species exhibiting shifts in COG in this direction. In all cases,
372 the thermal habitat COG moved further than the species COG. Hence, species distribution COGs
373 lagged slightly behind thermal COGs for all projected time periods, as indicated through a t-test
374 (Figure 6, Table S4). The strongest evidence for lags were during the first and last projection
375 periods ($p < 0.05$, mean first period = -0.010 °N/year, mean last period = -0.012 °N/year), while
376 there was less evidence of a lag during the middle projection period ($p = 0.08$, mean = -0.018
377 °N/year). As expected, there was no indication of a lag during the hindcast time period ($p > 0.1$,
378 mean = 0.003 °N/year).

379

380 **4 Discussion**

381 Climate change is already impacting oceanographic conditions in the Bering Sea (Stabeno &
382 Bell, 2019) and our results show that distributions of groundfish eggs and larvae in the Bering
383 Sea will continue to be affected by these changes over the next century. Early life stages of all
384 study species except Pacific cod are expected to shift geographically over time in response to
385 environmental shifts. Much of this change is seen through increased abundances of eggs and
386 larvae to the north or over the inner shelf area and Unimak Pass by the end of the century
387 (Figures 5, S5-S9). And, for many species, those regions were where initial analyses indicated
388 that increases in mean temperature would lead to positive effects on abundance. The direction of
389 movement or areas of high abundance are not consistent among species. Pollock, flathead sole,

390 and Alaska plaice are predicted to move northward in terms of the COG of their distributions,
391 which contrasts with the directions predicted for yellowfin sole (south), northern rock sole (east),
392 and Pacific cod (west; Table 2). These shifts, however, may still result in a mismatch between
393 species distributions and ideal habitat over time, as the species studied here overall lag behind
394 their thermal niche (Table S4). In addition, the distance between COGs for different life stages of
395 pollock, Alaska plaice, and flathead sole are predicted to change over time, possibly indicating a
396 shift in the overlap of egg and larval distributions and reduced connectivity between the two
397 habitats. Similar mismatches or increases in overlap may occur with predators or competitors,
398 and are predicted to occur globally (Bindoff et al., 2019). Our study provides new insight into
399 how groundfish species may be impacted by next-century changes in temperature and salinity,
400 though there are a number of other factors such as climate effects on ocean currents, fishing
401 pressure changes, and altered species interactions that were not evaluated here. In addition, we
402 were limited by the seasons during which data was collected, the uncertainty associated with
403 long-term climate projections (Brodie et al., 2022), and the application of correlative methods
404 like SDMs rather than mechanistic models. In the case of model method choice, mechanistic
405 models were not used due to their tendency to be computationally expensive and a lack of
406 knowledge for all study species needed to predefine the requisite parameters. Therefore, these
407 results provide initial context into how spawning distributions may change long-term in the
408 Bering Sea and give insight into effects on their associated fisheries, but also provide a
409 foundation for further methodological development.

410

411 Early life stages of many marine fish species occupy a dynamic, pelagic environment and the
412 planktonic egg and larval stages in particular are largely unable to control their movement and

413 thus are strongly influenced by the prevailing oceanography. This means that the environment
414 they inhabit during these critical life stages primarily depends on where or when adults choose to
415 spawn, given this may influence what currents eggs and larvae are subjected to, prey availability,
416 and whether early-stage juveniles can later access nursery grounds (Ciannelli et al., 2015). Our
417 results indicate that spawners of multiple groundfish populations in the Bering Sea may be
418 flexible with where they spawn more so than when, hence why we see predicted changes in
419 spatial distributions of eggs and larvae. This is consistent with results from recent research using
420 *in situ* data for Bering Sea groundfish distributions (Vary et al., 2023), but other studies have
421 shown phenological flexibility for some species during recent years (Nichol et al., 2019) and
422 earlier spawning in response to rising temperatures has been predicted broadly for spring
423 spawning species (Pauly & Liang, 2022). Geographic flexibility may be seen through shifts in
424 distribution across the Bering Sea shelf, as with pollock, or through increasingly concentrated
425 abundances of eggs or larvae in specific areas, as seen with flathead sole and yellowfin sole.
426 These end-of-century locations are often areas where increases in abundance were observed
427 when the effects of a rise in mean temperature were revealed by the spatial varying coefficient
428 term (Figures 4, S1-S4). For instance, the visible geographic shift of pollock may be primarily in
429 response to temperature changes; plots showed positive effects on abundance with increases in
430 temperature in areas where pollock eggs and larvae are predicted to move over the next century
431 (Figures 4, 5). Northern rock sole larvae provide another example of this, with their distribution
432 predicted to become concentrated north of the Alaska Peninsula by the end of the century (Figure
433 S8). This area is where positive temperature effects on northern rock sole occurred (Figure S4).
434 Given the more dynamic relationships many species have with temperature in contrast to salinity
435 (Figure 3), it is not unexpected that both collocated and annual thermal conditions play an

436 important role in driving distributions for most species. Consequently, warming in the Bering
437 Sea may lead to spatial shifts in groundfish spawning distributions that then alter food webs and
438 result in cascading effects throughout the ecosystem. There may be increased mismatches with
439 prey distributions along with new competition for resources and predation pressure if species
440 composition changes. Ultimately, thermally driven changes in pelagic early life stage
441 distributions and the potential geographic flexibility of groundfish spawning distributions have
442 broader implications for the Bering Sea region.

443

444 Despite the importance of temperature and the likelihood of future spatial shifts for early life
445 stages, thermal habitat is not always the primary driver nor are geographic shifts always the
446 predicted response. In the case of yellowfin sole, the reason for future shifts southeastward
447 toward Bristol Bay still appear somewhat related to temperature, but other factors may be
448 involved. High magnitude positive effects of temperature on yellowfin sole abundance were
449 located in the southeast Bering Sea near Bristol Bay despite present-day high abundances near
450 St. Matthew Island (Figures S3, S7). These areas with current high abundances of yellowfin sole
451 were associated with lower magnitude or no positive effects with increases in temperature.
452 Therefore, temperature may drive shifts in distribution in part but currently, other oceanographic
453 features such as higher salinity or the need for larval retention in specific areas may be more
454 influential. Yellowfin sole prefer shallow, coastal areas to spawn and are vulnerable to high
455 temperatures (Ciannelli et al., 2022; Wilderbuer et al., 1992), but given that salinity may
456 decrease in those areas following increased terrestrial ice melt (Pilcher et al., 2022), where
457 yellowfin sole move over the next century may also be associated with preferred, higher
458 salinities. They, and other species, may also prefer specific substrate and this could constrain

459 movement to new spawning locations. For many species, like yellowfin sole, complex
460 relationships between habitat characteristics are likely to drive distributional changes over the
461 next century (Vary et al., 2023).

462
463 Future loss of spawning habitat has been predicted for numerous species globally (Dahlke et al.,
464 2020), though many species have been shown to shift phenologically rather than geographically.
465 Here, Pacific cod was the only species for which the phenological variability model was selected,
466 but this is possibly due to data limitations. The EcoFOCI surveys typically occur during a
467 several-week period in late spring, and again in late summer, but may not have the intra-seasonal
468 frequency necessary to capture temporal shifts, leading to increased selection of the
469 geographically flexible model. For example, in contrast to our results, pollock stocks in the Gulf
470 of Alaska and Bering Sea have historically been shown to shift their spawn timing and retain
471 specific spawning sites (Bacheler et al., 2012; Rogers & Dougherty, 2019). In the Bering Sea, it
472 is possible that our inclusion of additional years of data compared to Bacheler et al. (2012) led to
473 this discrepancy in results. However, recent studies on adult pollock have found evidence of
474 northward shifts (Eisner et al., 2020; Stevenson & Lauth, 2019). Additionally, in many cases past
475 studies have focused on either phenological shifts or changes in geography, not both. Regardless,
476 the differences between these studies and our own warrant further research into using these data
477 to predict spawning distributions. This may involve the inclusion of additional criteria like egg
478 and larval developmental stage or use of joint SDMs for a full life cycle analysis, both of which
479 may reduce prediction uncertainty about the future distributions of marine fishes. Also,
480 mechanistic models, particularly those that predict where eggs or larvae are likely to drift given

481 changes in current patterns, may provide valuable insight by incorporating physical
482 oceanographic features that impact retention or transport.

483
484 The projected spawning distributions of our six study species combined with previous research
485 provides initial context as to how they will be affected by climate change throughout their life
486 cycle. A study on juvenile and adult stages for these species showed that direction of movement
487 was generally northward for pollock, flathead sole, yellowfin sole, and northern rock sole, while
488 Alaska plaice shifted southward and little discernible movement was seen for Pacific cod
489 (Rooper et al., 2021). Directional trends were consistent with our results for pollock, flathead
490 sole, and Pacific cod but not for Alaska plaice, yellowfin sole, and northern rock sole. This may
491 be due to species' use of specific spawning grounds while non-spawning adult distributions
492 differ in location. For example, yellowfin sole use the Bering Sea inner shelf to reproduce,
493 flathead sole spawn on the mid-shelf, and northern rock sole spawn in areas on the mid-shelf,
494 along the Alaska Peninsula, and near Unalaska Island (Lanksbury et al., 2007; Porter, 2021;
495 Porter & Ciannelli, 2018; Wilderbuer et al., 1992). Climate change may lead to spatial mismatch
496 between areas suitable to spawners and areas conducive to survival of early life stages. Previous
497 work found that for young-of-the-year pollock, the projected warmer conditions that support
498 greater abundances of eggs and larvae prevent the appearance of necessary food sources, leading
499 to poor recruitment (Mueter et al., 2011). Higher temperatures are also expected to benefit
500 pollock adult stages (Bacheler et al., 2012), but a bottleneck appears to occur at the juvenile
501 stage. However, decreases in the southern extent of sea ice coverage associated with warm
502 surface temperatures may be driving a shift in the northern Bering Sea from a benthic ecosystem
503 to one that is more often pelagic like the eastern Bering Sea (Grebmeier et al., 2006). Changes to

504 community structure may lead to more prey availability for juveniles to the north, which is also
505 the direction eggs and larvae are expected to shift over the next century. This further illustrates
506 the importance of evaluating climate change effects on all life stages, as habitat requirements
507 often change throughout the life of marine species. These types of contrasting responses to
508 environmental conditions at different points in an organism's life cycle are likely exhibited by
509 other marine species.

510

511 Positive effects on abundance in response to higher water temperatures were seen during model
512 parameterization and spawning distributions are expected to have geographic flexibility in the
513 future. However, there was evidence for a lag in spawning distributions behind suitable thermal
514 habitat location during the projection time periods, albeit this was somewhat less evident during
515 the middle time period. This contrasts with the results of Pinsky et al. (2013), where the authors
516 found that marine species in multiple regions tend to track climate velocity. However, their focus
517 was on historic range shifts and later life stages, which are capable of directed movement toward
518 more favorable conditions unlike the planktonic early life stages that were examined in this
519 study. Future changes to ocean temperature may be more extreme than in recent decades and
520 here we explore a much longer time period, both of which may partially explain our observation
521 of lags. Additionally, it is possible that given the narrow thermal requirements of early life stages
522 and spawning adults, these stages may not be able to track climate as well as the non-spawning
523 adults and juveniles that were the focus of Pinsky et al. (2013). This may also illustrate future
524 mismatches and reduced connectivity between life stages and their stage-specific habitats,
525 possibly preventing life cycle completion for some species. Moreover, our study did not include
526 other important oceanographic conditions such as current velocity, water density, and salinity in

527 our assessments of changing suitable early life history habitats over time, all of which may affect
528 ichthyoplankton distributions (Bashevkin et al., 2020). And for spawning adults, conditions at
529 the seafloor may not continue to match appropriate early life stage habitats in the near-surface,
530 pelagic environment. Despite this, determining projected species intersections with thermal
531 habitat provides important insight into the future ability of these species to inhabit areas with
532 biologically suitable temperatures.

533

534 Projecting species distributions remains an active area of research and it remains challenging to
535 predict how species will respond to climate change. Our research provides insight into potential
536 changes in spawning distributions but methodological improvements are needed. As pointed out
537 by Barnes et al. (2022) there are issues with using complex SDMs that include terms like
538 spatially varying coefficients, which allow abundance over time or space to vary with ocean
539 conditions. However, use of these terms allowed us to investigate tradeoffs between geographic
540 and phenological variability at the spawning stage, something less relevant to the adult
541 populations of the two species examined by Barnes et al. (2022). We constrained our models
542 using a similar methodological approach to prevent extrapolating beyond conditions experienced
543 in the hindcast time period. While this prevents overfitting, it also prevents us from
544 understanding how species will respond to novel conditions like higher water temperatures.
545 Inclusion of extreme years has been shown to improve predictions for some species and life
546 stages (Muhling et al., 2020), but when using conditions derived from the higher emissions
547 scenario, this may not fully alleviate the issues associated with extrapolation or certain life stages
548 of some species. More mechanistic studies may be useful for pinpointing suitable habitat for
549 each life stage, along with further development of SDMs for use in projections.

550

551 Our research not only adds to a small body of literature on early life stage distributional
552 responses to climate change, but it also has implications for future fishery management and
553 applications to other regions. Understanding potential changes to spawning distributions
554 connects directly to many fisheries, including pollock. This fishery operates with two seasons,
555 the first occurring during the winter months and focused on targeting spawning aggregations to
556 harvest roe (egg masses). Previous work found that variations in fishery spatial distribution for
557 pollock are more strongly associated with overall fish abundance, financial factors, and annual
558 temperature fluctuations rather than climate regimes, and that shifts for the roe fishery are
559 typically temporal (Haynie & Pfeiffer, 2013). While there have yet to be observed northward
560 shifts in the pollock roe fishery (Haynie & Pfeiffer, 2013; Watson & Haynie, 2018), if spawning
561 aggregations indeed move northward as suggested by our results, the fleet may eventually
562 follow. This response by the fishery is uncertain due to the numerous factors influencing fleet
563 dynamics, but could occur in other fisheries where spawning aggregations are targeted and range
564 shifts are observed. For example, Atlantic mackerel spawning distributions expanded northward
565 over several decades, resulting in potential challenges for transboundary fishery management
566 (Bruge et al., 2016; Chust et al., 2023). Shifts in spawning or adult distributions may also lead to
567 difficulty accessing fishing grounds, in part from increased fuel costs due to increases in distance
568 traveled. Our study showed that multiple species are expected to shift northward, away from the
569 Alaska Peninsula and Aleutian Islands, where most of the ports for these fisheries are located.
570 These shifts may lead to changes in fishing ground locations. Future analyses using methods like
571 these in other regions with sufficient early life stage fishery data can provide important insights
572 into future fishery and ecosystem effects as our oceans continue to change. While there are

573 limitations to our methodologies, our results illustrate the importance of evaluating climate
574 effects on early life stages of marine species and the need for further research beyond the Bering
575 Sea.

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Data Availability Statement

The scripts that support the findings of this study are openly available in Zenodo at DOI: 10.5281/zenodo.10565114.

Conflict of Interest Statement

The authors declare no conflict of interest.

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Tables

Table 1: This table shows the best fit model selected during the parameterization process. The difference in AIC was calculated between Equation 2 and the best model. Deviance is the percent deviance explained by the best model.

Species	Stage	Best Model	Δ AIC	Deviance
Pollock	Eggs	$g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(\phi, \lambda, by = T)$	368	52.9%
	Larvae	$g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(\phi, \lambda, by = T)$	1009	53.1%
Flathead Sole	Eggs	$g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(\phi, \lambda, by = T)$	217	52.9%
	Larvae	$g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(\phi, \lambda, by = T)$	603	68.6%
Alaska Plaice	Eggs	$g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(\phi, \lambda, by = T)$	156	56.5%
	Larvae	$g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(\phi, \lambda, by = T)$	702	68.8%
Yellowfin Sole	Larvae	$g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(\phi, \lambda, by = T)$	211	76.7%
Northern Rock Sole	Larvae	$g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(\phi, \lambda, by = T)$	260	52.0%
Pacific Cod	Larvae	$g(CPUE) = re(y) + te(\phi, \lambda) + s_1(J) + s_2(SST) + s_3(SSS) + s_4(J, by = T)$	160	54.9%

Table 2: Change in COG for each species and life stage over time. The direction of movement indicates the COG location during the 2070-2099 time period relative to the hindcast time period. The distance reflects how far the COG moved in kilometers between the hindcast and 2070-2099.

Species	Stage	Direction	Δ Distance (km)
Pollock	Egg	NE	119.5
	Larvae	NW	109.8
Flathead Sole	Egg	NE	78.4
	Larvae	NW	145.7
Alaska Plaice	Egg	N	66.1
	Larvae	NW	216.8
Yellowfin Sole	Larvae	SE	247.5
Northern Rock Sole	Larvae	E	135.3
Pacific Cod	Larvae	W	26.1

Figure Legends

Figure 1: Map of the study region with relevant locations labeled.

Figure 2: Average change in temperature over the Bering Sea shelf during the historical period (1980-2014) and the projection period (2015-2099). Each plot is for an ESM and shows the historical values (yellow) as well as both SSPs (red and blue). Shading indicates minimum and maximum values of temperature.

Figure 3: The first three columns depict partial dependence plots for day of year, SST, and SSS for hindcast models for each species and stage, with the same axis ranges for a given species. The last two columns represent an estimate of the varying coefficient terms with regard to temperature. The fourth column depicts how phenology would change with a 1°C increase (purple) in mean shelf temperature. The fifth column depicts how a 1°C increase in temperature would change the spatial distribution of a species. Purple indicates a decrease in abundance; orange indicates an increase.

Figure 4: Maps of the effect of an increase in mean temperature on abundance of pollock eggs and larvae imposed over teal shading depicting their average predicted spatial distribution during the hindcast time period. Red bubbles indicate increases in abundance with an increase in temperature while blue bubbles indicate a decrease in abundance with a decrease in temperature. Bubble size indicates the magnitude of the effect of temperature. Areas without bubbles indicate no statistically significant change in abundance at that location with a change in temperature.

Figure 5: Maps of projected distributions of pollock eggs (top) and larvae (bottom) over the next century for three time periods for each SSP. Abundance is scaled from 0 to 1, with lighter colors indicating higher abundance. The projections using the three ESMs were averaged for each SSP and time period to create the final maps.

Figure 6: Plots of COG for each species and stage (solid line) as well as their corresponding thermal niche (dotted line) over the hindcast and projection time periods. Solid circles represent different COGs, with colors corresponding to the time periods.