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Climate change and the future productivity and distribution of crab in the Bering Sea

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Crab populations in the eastern Bering Sea support some of the most valuable fisheries in the United States, but their future productivity and distribution are uncertain. We explore observed changes in the productivity and distribution for snow crab, Tanner crab, and Bristol Bay red king crab. We link historical indices of environmental variation and predator biomass with observed time series of centroids of abundance and extent of crab stock distribution; we also fit stock–recruit curves including environmental indices for each stock. We then project these relationships under forcing from global climate models to forecast potential productivity and distribution scenarios. Our results suggest that the productivity of snow crab is negatively related to the Arctic Oscillation (AO) and positively related to ice cover; Tanner crab's productivity and distribution are negatively associated with cod biomass and sea surface temperature. Aspects of red king crab distribution and productivity appear to be related to bottom temperature, ice cover, the AO, and/or cod biomass. Projecting these relationships forward with available forecasts suggests that Tanner crab may become more productive and shift further offshore, red king crab distribution may contract and move north, and productivity may decrease for snow crab as the population contracts northward.

Keywords: Bering Sea, climate change, crab, fisheries, productivity, species distribution

Introduction

Bering Sea crab fisheries are some of the most economically important fisheries in the United States (Figure 1) and are consistently in the top 15 US fisheries in terms of value [National Marine Fisheries Service/National Oceanic and Atmospheric Administration (NMFS/NOAA), 2019]. Ten stocks of five species are assessed and managed in the Bering Sea: red king crab (*Paralithodes camtschaticus*; Bristol Bay, Norton Sound, Pribilof Islands, Western Aleutian Islands), snow crab (*Chionoecetes opilio*; Bering Sea), Tanner crab (*Chionoecetes bairdi*; Bering Sea), blue king crab (*Paralithodes platypus*; Saint Matthews Island, Pribilof Islands), and golden king crab (*Lithodes aequispinus*; Aleutian Islands, Pribilof Islands). These fisheries are male only and have limitations on the size of crab retained. Crab fisheries in the Bering Sea produced an average of 36 000 tonnes of crab over the last 5 years, worth an average of $219 million [National Marine Fisheries Service/National Oceanic and Atmospheric Administration (NMFS/NOAA), 2019]. However, combined catches have been as high as 160 000 tonnes (1993, driven primarily by snow and Tanner crab) and as low as 18 500 tonnes (2001). Combined value has been as high as $265 million (also in 1993) and as low as $51 million (1984). These catches and associated
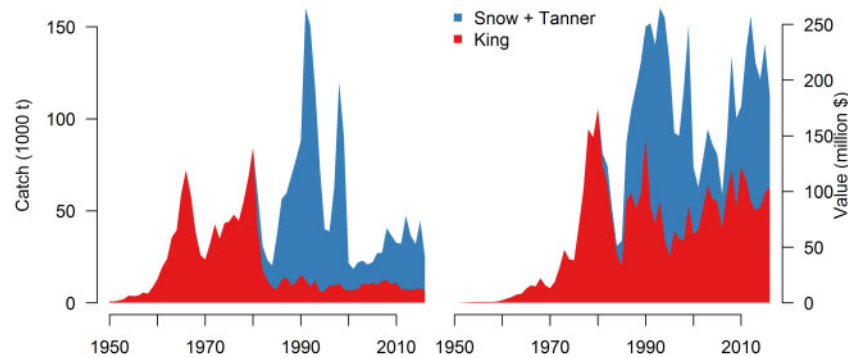
Figure 1. Catches and values for US king crab and snow crab fisheries. Snow and Tanner crab are combined (but exclude "Southern" Tanner crab, coming from fisheries south of the Bering Sea). King crab includes all king crab species (red, blue, golden). Reported from https://www.st.nmfs.noaa.gov/commercial-fisheries/; accessed July 2018.

values are primarily derived from the snow crab, Tanner crab, and Bristol Bay red king crab fisheries, which account for >92% of catch over the last 5 years.

Variability in catch of crab in the Bering Sea is related to variability in population sizes and changes in management. Survey data indicate that the average density of commercial males has ranged from ~200 to 2900 snow crab individuals per square nautical mile, ~20 to 480 Tanner crab, and ~10 to 110 red king crab individuals (Figures 2–4; these densities are not subject to adjustments by catchability of the survey or weight of crab—see the individual assessments for the discussion of this point). Tanner crab and snow crab have been previously declared overfished (in 1998 and 2010 for Tanner crab and 1999 for snow crab; NPFMC (North Pacific Fishery Management Council), 2000, 2012) but have since been rebuilt. Changes in management after the overfished declarations have reduced and stabilized catches for snow crab and Tanner crab. The overfished declarations of these stocks were likely due to the combined effect of removals via the fisheries and changes in productivity based on environmental forcing. Declines in recruitment for each stock that did not appear to be related to changes in spawning biomass preceded the drops in biomass that triggered rebuilding plans (Stockhausen, 2019; Szuwalski, 2019).

The relative influence of fishing and the environment has been a central theme of fishery science over the last 100 years, and considerable effort has gone into understanding the drivers of recruitment dynamics in exploited marine fisheries (Hjort, 1914; Lasker, 1978; Cury and Roy, 1989; Cushing, 1990; Jacobson and MacCall, 1995; Myers, 2001). Recent meta-analyses suggest that spawning biomass is often not a key driver of recruitment over the observed range of stock sizes (Cury et al., 2014), non-stationary dynamics may be common (Britten et al., 2016; Szuwalski and Thorson, 2017), and shifts in recruitment unrelated to spawning biomass for stocks within the same large marine ecosystem sometimes co-occur with changes in environmental indices (Szuwalski et al., 2015). In spite of relatively conservative harvest policies, several fished crab populations in the Bering Sea are declining. The observed number of commercially-sized (>101 mm) snow crab males in the summer survey was at an all-time low in 2017 (though a large recruitment pulse now appears to be entering the population; Szuwalski, 2019). The area-swept estimate of total biomass from the National Marine Fisheries Service (NMFS) survey was the lowest

on record (beginning in 1975) for Bristol Bay red king crab in 2018 (Zheng and Sideek, 2019). Estimated Tanner crab survey biomasses are also low and declining (Stockhausen, 2019). Saint Matthews blue king crab was designated overfished in 2018, and other smaller and currently unfished crab populations in the Bering Sea have not rebounded to previously seen abundances (e.g. Pribilof Islands blue king crab; Stockhausen, 2019). Observed population declines under conservative (or absent) removals can suggest an influence of environmental conditions on stock productivity (Hollowed et al., 2020; Reum et al., 2020).

Climate change is expected to produce large impacts on ocean temperature and ocean productivity in high latitude systems (Arrigo and Van Dijken, 2015; Barange et al., 2018; Smith et al., 2019; Meredith et al., in press). In the Bering Sea, the changes will likely impact some of the critical physical characteristic of the ecosystem, including seasonal ice cover, distinct biophysical domains driven by surface forcing and tidal mixing, ice associated spring ice algal and phytoplankton blooms, and fall phytoplankton blooms (Hunt et al., 2011; Baker and Hollowed, 2014; Stabeno et al., 2017). Regional projections for these indices suggest decreasing ice cover, increases in surface and bottom temperatures, and changes in algal blooms relative to historical conditions (Hermann et al., 2019).

These environmental changes will have consequences for the species living in the Bering Sea (Holsman et al., 2018). For example, the role of temperature and sea ice on the seasonal availability of high energy content planktonic prey (large zooplankton) has been related to overwintering success of pollock and cod, two abundant and economically important species (Heintz et al., 2013; Duffy-Anderson et al., 2017). Shifting trophic demand and changes in overwintering success have already been observed in pollock (Heintz et al., 2013; Holsman et al., 2019). Ocean acidification is projected to influence crab stocks and pelagic forage species (Comeau et al., 2010; Long et al., 2013). Species interactions are changing (Spencer et al., 2016; Reum et al., 2020) and spatial distributions are shifting as a result of changing bottom temperatures (Barbeaux and Hollowed, 2019; Stevenson and Lauth, 2019; Thorson, 2019). Overall system productivity is also projected to change in response to warming (IPCC, 2014; Holsman et al., 2018; Hermann et al., 2019).

In addition to changes in productivity, changes in distribution resulting from changes in environmental drivers can affect the functioning of a fishery and the effectiveness of management.
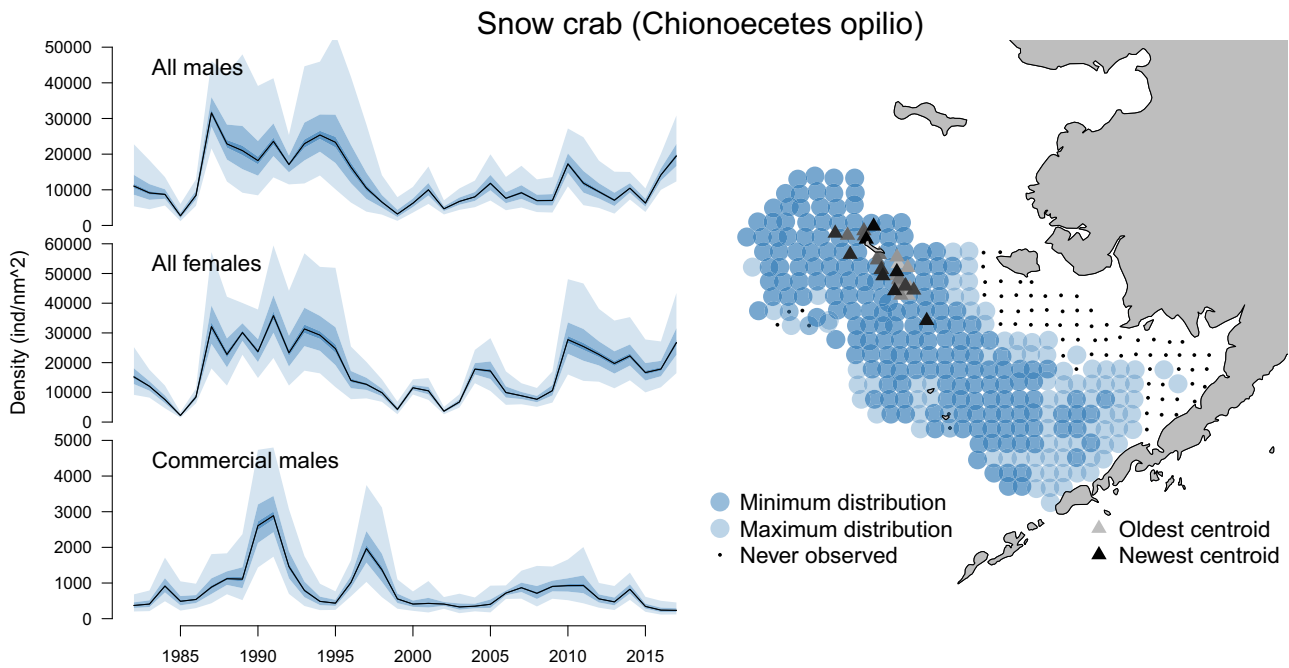
Figure 2. Distribution and density estimates from the NMFS summer bottom-trawl survey for snow crab in the Bering Sea. Density estimates are produced from unstratified extrapolation of the mean density in a given years and presented with polygons representing the 5th to 95th (light coloured polygon) and 25th to 75th quantiles (dark polygon), based on calculated standard errors. Commercial males are males >101 mm carapace width. Dark lines are the point estimates in a given year. Each dot in the map (right) represents a survey station; xcoloured dots represent the maximum distribution observed (i.e. each station in the year in which the most survey stations reported a positive catch are represented as light dots) and the minimum distribution observed (i.e. each station in the year in which the fewest survey stations reported a positive catch are represented as dark dots). Small black dots indicate stations at which the species has never been observed. Triangles represent the centroid of abundance over time.
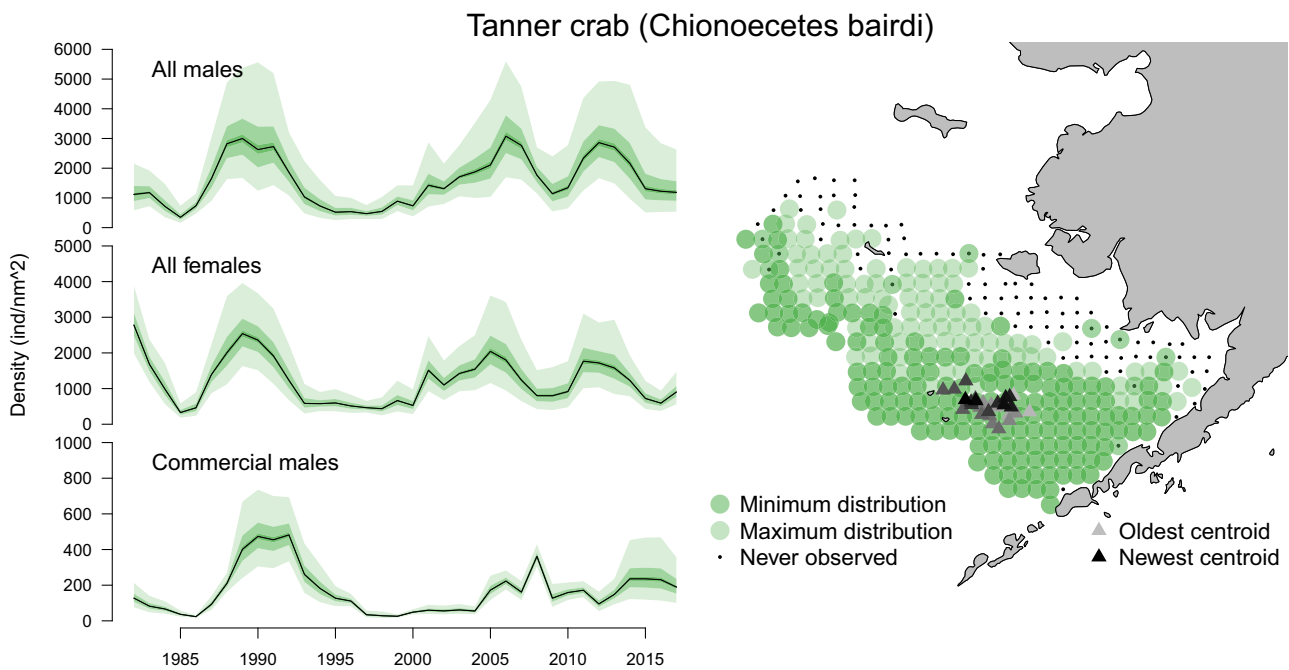

Figure 3. Distribution and density estimates from the NMFS summer bottom-trawl survey for Tanner crab in the Bering Sea. Commercial males are >127 mm carapace width.
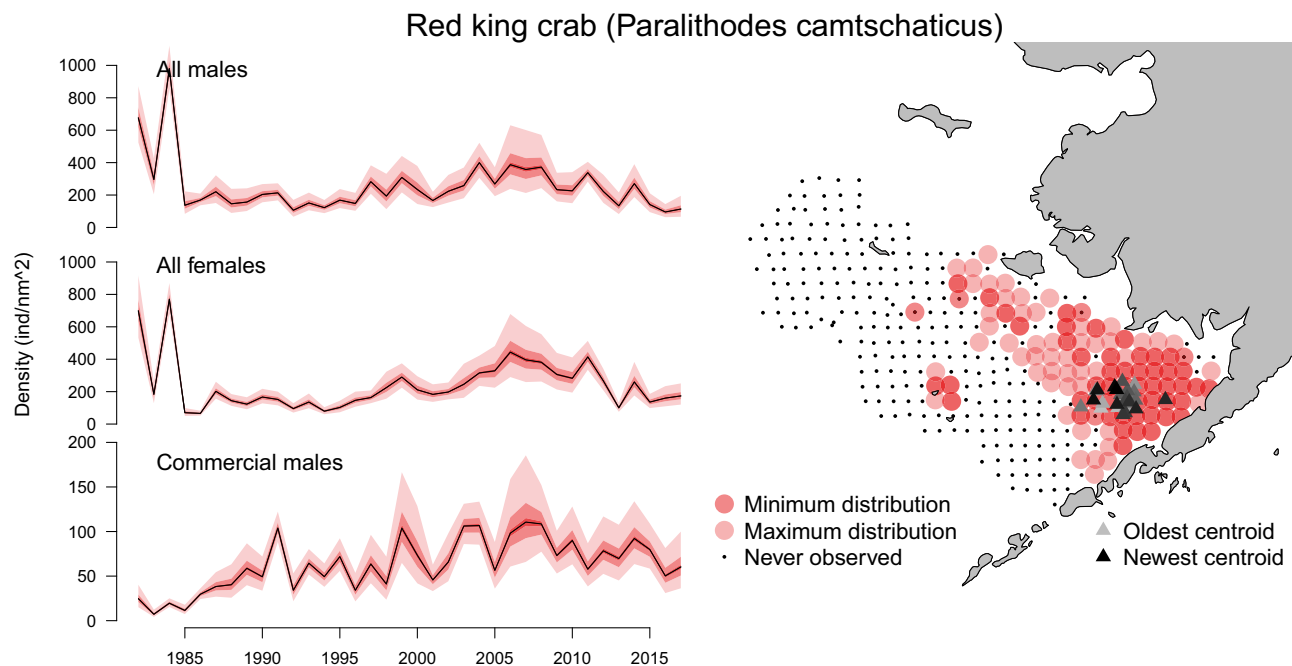
Figure 4. Distribution and density estimates from the NMFS summer bottom-trawl survey for red king crab in the Bering Sea. Commercial males are >135 mm carapace length.

Contraction or expansion of a population can change the profitability of a fishery by altering the necessary fuel to reach fishing grounds (Haynie and Pfeiffer, 2013). Populations that expand beyond surveyed areas can be difficult to assess and calculate management reference points (Szuwalski and Hollowed, 2016; Thompson and Thorson, 2019). Changes in density-dependent effects on growth or mortality (for example) may also be related to changing environmental conditions (Stawitz *et al.*, 2015). Changes in these vital rates can further compound difficulties in calculating reference points to inform management (Szuwalski *et al.*, 2018). Globally, exploited marine populations often track the changes in environmental conditions and there is evidence that this is occurring in the Bering Sea as well (Pinsky *et al.*, 2013).

A considerable body of literature has been devoted to the drivers of productivity and distribution of crab in the Bering Sea. Snow crab recruitment has been linked to bottom temperature and advection paths (Zheng and Kruse, 2006; Parada *et al.*, 2010), phytoplankton blooms (Burgos *et al.*, 2013), the Pacific Decadal Oscillation (PDO) (Szuwalski and Punt, 2013), and shifts of spatial distribution (Zheng and Kruse, 2006). Snow crab distribution has been linked to advection patterns and an "environmental ratchet" by which fishing and the environment slowly interact to elicit a contraction of the population that is difficult to reverse (Orensanz *et al.*, 2004). Distributions of female snow crab have been linked to thermal gradients (Ernst *et al.*, 2005). Variability in Tanner crab recruitment in the eastern Bering Sea has been linked to wind direction and other influences on advection pathways and appears to be highly reliant on local retention (Rosenkranz *et al.*, 1998; Richar *et al.*, 2015). While no strong relationship has been found between recruitment and spawning stock size (Zheng and Kruse, 2000), spatial patterns of recruitment may be dependent on the spatial distribution of spawning females due to the importance of local retention (Richar *et al.*,

2015). Growth and survival decrease below 3°C for early benthic stages of Tanner crab; thus, recruitment variability and spatial distribution on the eastern Bering Sea shelf may also be related to the distribution of cold bottom water (the "cold pool") in the middle domain of the shelf (Paul and Paul, 2001; Richar *et al.*, 2015; Ryer *et al.*, 2016). The spatial distribution of Bristol Bay red king crab has been associated with bottom temperature and the PDO (Loher and Armstrong, 2005; Zheng and Kruse, 2006); northerly shifts of distribution are generally associated with warmer temperatures and high values of the PDO. Red king crab recruitment may be linked to the Aleutian Low, with crab larval survival and subsequent recruitment being negatively impacted by strong winter Aleutian Lows (Zheng and Kruse, 2000, 2006). Red king crab recruitment strength in Bristol Bay may also be negatively affected by shifts in the spatial distribution of mature females over time that have made it difficult to supply larvae to their southern nursery area (Zheng and Kruse, 2006).

Our goal here is to examine the historical influence of environmental variation in these stocks with the most up-to-date data and then project observed relationships to develop potential scenarios for productivity and distribution under climate change for the three largest crab stocks in the Bering sea: snow crab, Tanner crab, and Bristol Bay red king crab. We identify relationships between indices of environmental variation with yearly centroids of abundance and extent of stock distribution and then fit stock–recruit curves with and without environmental indices for each stock. We use our identified relationships with regional projections from global climate models (GCMs) to forecast potential productivity and distribution scenarios for each stock. We conclude by discussing the implications of projected productivity and distribution scenarios for the assessment and management of these stocks and research needed to better understand the response of these stocks to a changing environment.

Methods

Population data

Starting in the early 1970s, the Alaska Fisheries Science Center (NOAA Fisheries Service, US Department of Commerce) has conducted an annual multispecies bottom-trawl survey on the eastern Bering Sea shelf during the summer in the Bering Sea (Lauth and Nichol, 2013). Relatively major changes in methodology occurred in 1975 (initial standardization), 1982 (gear) and 1988 (survey coverage and number of stations). As a consequence of these changes in survey gear and areal coverage, we used only data collected since 1989 in our analysis of patterns in spatial distribution to support comparability between yearly measures. Since 1988, the bottom-trawl survey has been conducted on a fixed grid at 375 stations (Figure 2) by two vessels using identical gear (83–112 otter trawls with an 83-ft headrope and a 112-ft footrope; Lauth and Nichol, 2013). The survey begins in Bristol Bay in late May or early June and 4–6 stations are typically sampled each day by two vessels each, moving westward across the shelf and northward past St. Matthew Island prior to completion in early August. In years when colder water temperatures have delayed the red king crab reproductive cycle, a portion of the inner Bristol Bay area is re-sampled after the standard survey is completed to adequately sample female red king crab (Lauth and Nichol, 2013). Net mensuration equipment and bottom contact sensors are used to monitor the survey gear's fishing performance and area swept at each survey station. Surface and bottom water temperatures, as well as bottom depth, are also measured for each survey tow. All crab are removed from the catch in each tow and sorted by species and sex, and a total catch weight is obtained for each species. Data recorded for individual crab include carapace width (Tanner and snow crab) or length (all king crab species), shell condition, and (for females) maturity state, clutch size, egg condition, and egg colour (Land *et al.*, 2018). While most crab caught are measured for individual characteristics, a random subsample of individuals of a species is taken when a particularly large catch (>300 crab) is made.

Yearly centroids of male abundance in terms of latitude and longitude ($C_{y,lat}$, $C_{y,lon}$) were calculated from the described survey data above. Centroids were calculated by taking an average of the latitude and longitude of survey stations ($lat_{y,t}$ and $lon_{y,t}$), weighted by the density of a given crab species observed at each station ($d_{y,t}$):

$$C_{y,lon} = \frac{\sum_t (d_{y,t} lon_{y,t})}{\sum_t d_{y,t}}. \tag{1}$$

The centroid for latitude was calculated in the same way as for longitude (1). Selectivity of small crab is poor in the NMFS survey gear, so larger crab are "overrepresented" in the calculations of density. However, selectivity is not thought to have changed over our study period, so the centroid should be a consistent measure of the position of the population over time (while recognizing spatial ontogeny can influence the outcome; Barbeaux and Hollowed, 2019). The number of stations at which crab of each species were observed is used as a measure of the distributional extent of the stock in a given year. Estimates of recruitment and female spawning biomass were taken from the most recent stock assessments for snow, Tanner, and Bristol Bay red king crab (Szuwalski, 2019; Stockhausen, 2019; Zheng and Sideek, 2019). Female spawning biomass was used as a proxy of reproductive

potential in this analysis, but females are not a target of the fishery. Consequently, it is possible that sperm limitation could be an issue in using female spawning biomass as a proxy for reproductive potential, but research suggests that this is not the case for snow crab at least (Rugolo *et al.*, 2005).

Estimates of recruitment were lagged to the year of fertilization for each stock for use in the analysis (5, 5, and 6 years for snow, Tanner, and red king crab, respectively). Using the estimates of recruitment from the assessment is more appropriate than using measures of small crab from the survey for several reasons. First, assessments incorporate other sources of information (e.g. length composition data) that can support the determination of cohort size. The smallest crab are also poorly selected in the survey gear, so there can be years in which the survey data appear to show a large cohort being established, but subsequent length composition data suggest measurement error contributed to the "observation" of a large cohort. Even within the assessment, a new cohort must be observed for several consecutive years before the uncertainty around its size is reduced. The assessment relies on some assumptions (e.g. invariant growth and natural mortality over time and space) to produce estimates of recruitment, but we think the benefits of incorporating multiple sources of data and the ability to account for measurement error in the survey data outweigh the potential pitfalls of these assumptions.

Historical environmental data

Data for local environmental variables and large-scale indices of environmental variation were collated from the National Oceanic and Atmospheric Administration's "Bering Climate" data portal (NOAA, 2019). Both local indices and large-scale indices were included in the analysis (Figure 5). Local indices were chosen to represent variation hypothesized to potentially influence crab population dynamics based on previous studies. Ice cover, sea surface temperature (SST), and bottom temperature are related to the size of the cold pool and, to some extent, the magnitude of spring plankton blooms, both of which are thought to influence crab productivity in the Bering Sea (Parada *et al.*, 2010). Crab are a known component of cod diet, consequently cod spawning biomass was included here as a potential covariate (Figure 5d). The size at maturity roughly represents the size of cod for which crab begin to appear in the diet of cod (Burgos *et al.*, 2013).

Large-scale indices included in our analysis are linked to these local processes and also incorporate atmospheric forcing. Indices of large-scale variation can capture the prevailing "state" of the ecosystem in ways that single local variable cannot and consequently sometimes predict ecological processes better than local variables (Hallett *et al.*, 2004). The PDO and the Aleutian Low were included in this analysis based on previous studies linking them to crab recruitment in the Bering Sea (Zheng and Kruse, 2006; Szuwalski and Punt, 2013), and other large-scale indices related to the formation and retention of sea ice were also included in the analysis [the Arctic Oscillation (AO) and the Alaskan Index]. Local and large-scale indices were lagged to the year of larval release because environmental effects are thought to influence the larval phases most strongly; cod biomass was lagged to 3 years post-fertilization to roughly match the size at which crab are observed in the diet of cod (Burgos *et al.*, 2013).
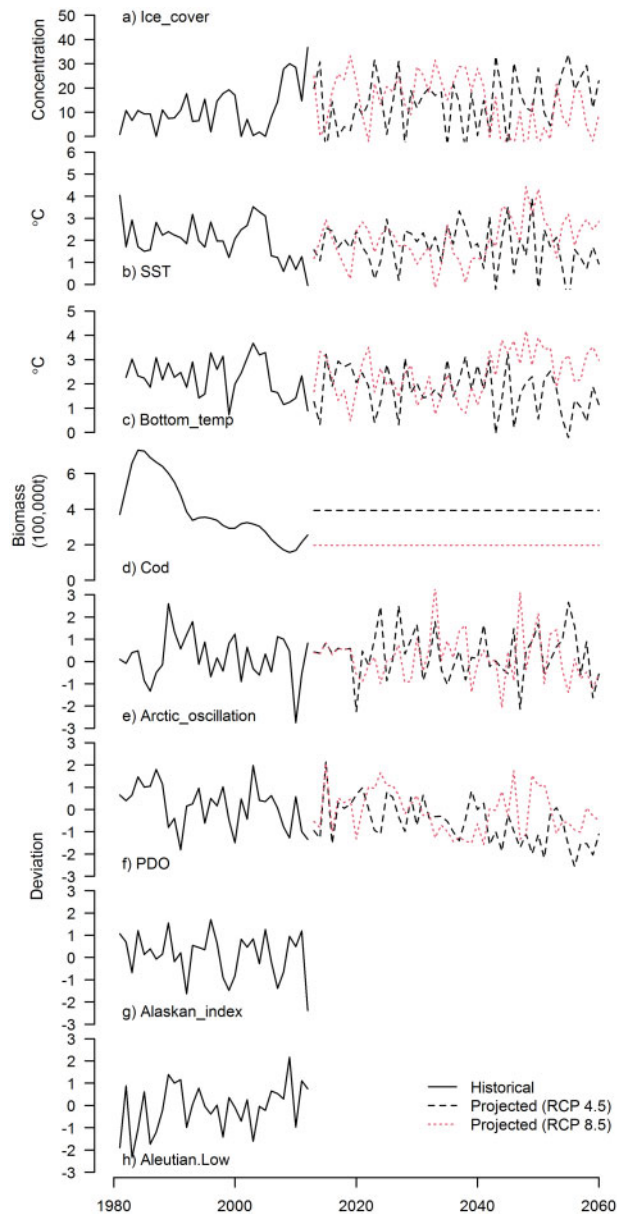
Figure 5. Historical environmental conditions and projections. Projections for cod do not align with an RCP path but are the mean spawning biomass over the historical period and half of that. Projections were unavailable for the Alaskan Index and Aleutian Low, but these were not included in the best model for any response variable.

Modelling framework

Linear models were fit to the latitudinal and longitudinal components of the time series of centroids of abundance and the extent of distribution calculated from the survey data for each species (2). Indices of environmental variation, I, were tested as explanatory variables and α and β were estimated parameters. For example:

$$C_{lon} = \alpha + \beta I + \varepsilon; \ \varepsilon = N(0, \sigma). \quad (2)$$

Thirty-six models were tested for each dependent variable, including no more than three explanatory variables each. At most,

each model contained a local variable, cod biomass, and a large-scale index of environmental variation (see Figure 1 for a summary of the models tested and Supplementary Figure S1 for correlations between variables). This was done to decrease the number of models analysed, avoid incorporating collinear variables in the same model, and minimize the potential for multiple tests to identify spurious relationships. The null model for comparison is the mean over time.

A similar model development scheme was implemented to test variables for explanatory power in species-specific stock–recruit curves. The natural logarithm of the ratio of recruits, R, to female spawning biomass, S, was modelled as a linear function of female spawning biomass, S, and other environmental variables, I, in the form of a linearized Ricker curve (3) (Ricker, 1954), in which α and β were estimated parameters. A Ricker model with no environmental variables was used as a baseline to which other models were compared (4).

$$\log\left(\frac{R}{S}\right) = \alpha + \beta_1 S + \beta_2 I + \varepsilon; \ \varepsilon = N(0, \sigma), \quad (3)$$

$$\log\left(\frac{R}{S}\right) = \alpha + \beta S + \varepsilon; \ \varepsilon = N(0, \sigma). \quad (4)$$

Akaike's corrected information criterion (AICc; Burnham and Anderson, 2002) was used to parsimoniously evaluate the addition of environmental covariates in all of the models tested. The change in AICc relative to a model with no environmental covariates (ΔAICc) is reported here as a measure of the tradeoff between improvements of fit and the addition of estimated parameters linking the environment to productivity or distribution.

Cross validation

Leave-one-out cross validation (LOOCV) was performed for models in which including an environmental index produced a model with a lower AICc than the null model. LOOCV was accomplished by sequentially dropping one observation from the data used to fit the model, fitting the model, then recording the r-squared value of the model in which all the data are included in the objective function as a measure of model fit.

Projections of productivity and distribution

Regional dynamically downscaled models produce high-resolution estimates of bottom temperature and SST that more closely match observations than estimates from global models (Hermann *et al.*, 2016). In collaboration with partners, the Alaska Climate Integrated Modeling (ACLIM) project (Hollowed *et al.*, 2020) recently produced high-resolution downscaled projections of oceanographic and lower-trophic level conditions in the Bering Sea using the Regional Ocean Modeling System (Shchepetkin and McWilliams, 2005; Haidvogel *et al.*, 2008; Hermann *et al.*, 2019). The regional ocean downscaled simulations were driven by atmospheric forcing and ocean lateral boundary conditions from selected GCMs that participated in the Coupled Model Intercomparison Project phase 5 (Taylor *et al.*, 2012); in particular, ACLIM considered GCM forcing under Representative Concentration Pathways (RCP) 4.5 (moderate carbon emission scenario) and 8.5 (high carbon emission

scenario) (Hermann *et al.*, 2019). Regional downscaling from global GFDL-ESM2M forcing was used in this analysis.

For each projection, the National Marine Fisheries Service Alaska Fisheries Science Center annual summer bottom-trawl survey was replicated in time and space (using historical mean survey date at each latitude and longitude of each gridded survey station) to derive estimates of sea surface and bottom temperatures (Figure 5). All index projections were bias corrected to the 2006–2017 downscaled realizations under present-day conditions (hereafter "hindcast") period using the delta method (see Holsman *et al.*, 2019; Hollowed *et al.*, 2020) assuming unequal variance in the GCM projections and hindcast (Ho *et al.*, 2012; Hawkins *et al.*, 2013) such that:

$$T_{\text{fut},y} = \overline{T}_{\text{hind},\rightarrow\text{ref}} + \frac{\sigma_{\text{hind},\rightarrow\text{ref}}}{\sigma_{\text{fut},\rightarrow\text{ref}}}\left(T_{\text{fut},y} - \overline{T}_{\text{fut},\rightarrow\text{ref}}\right), \tag{5}$$

where $T_{\text{fut},y}$ is the raw projected timeseries, $\overline{T}_{\text{hind},\rightarrow\text{ref}}$ is the mean of the hindcast during the reference years $\rightarrow$ ref (2006–2017), $\overline{T}_{\text{fut},\rightarrow\text{ref}}$ is the average of the raw projected timeseries during the reference years $\rightarrow$ ref, $\sigma_{\text{hind},\rightarrow\text{ref}}$ is the standard deviation of the hindcast during the reference years $\rightarrow$ ref, $\sigma_{\text{fut},\rightarrow\text{ref}}$ is the standard deviation of the raw projection timeseries during the reference years $\rightarrow$ ref, and $T_{\text{fut},y}'$ is the final bias-corrected projected timeseries.

Projections of the PDO and the AO (also known as the Northern Annular Mode) were obtained from the GCM GFDL-ESM2M (Dunne *et al.*, 2012). The first EOFs of SST and sea level pressure, obtained over the Northern Pacific Ocean and Northern Hemisphere from reanalysis datasets [HadISSTv1.1 (Rayner *et al.*, 2003) and NOAA-CIRES 20CR (Compo *et al.*, 2011), respectively] for a historical period (1900–2005), were to obtain the associated principal component time series, which were then used as the projections of the PDO and the AO indices in this study. The detailed description for the methodology can be found in Lee *et al.* (2019).

We used two potential scenarios for projected cod bioamss: an "average cod" scenario in which the projected spawning biomass was ∼390 000 tonnes and a "low cod" scenario in which cod was one half of the average of historical spawning biomass (19 500 tonnes). "Low cod" projects cod at a similar biomass to the 2018 assessment estimate, which is also close to the minimum stock size threshold for the stock (192 000 tonnes; Thompson and Thorson, 2019).

Projections of the stock–recruit relationships also require a projection of spawning biomass; we used the mean of the spawning biomass over the historical period for each stock in the projections presented here. This ignores the influence of recruitment on spawning biomass going forward and may also be an accurate representation of the future given one of the objectives of the sloped control rule used in management is to maintain spawning biomass near a target biomass. The target biomasses for the three stocks in the analysis are close to the average spawning biomass over the historical period.

Results

Historical analysis

Including environmental variables in spawner-recruit curves improved the fit for all three crab stocks, but variability in measures of distribution was not improved by incorporating environmental

variables for all stocks (Table 1). The best model for snow crab recruitment included ice cover and the AO (ΔAICc of −7.73 compared to the base stock–recruit curve; Table 1). Ice cover was positively related to recruitment; poor recruitment was associated with positive values of the AO. The latitude and longitudes of centroids of abundance were significantly better explained by including the AO (longitude and latitude) and SST (latitude), but the distributional extent of snow crab was not better explained by including environmental variables.

Bottom temperature and cod biomass were the two most important factors associated with Tanner crab recruitment (ΔAICc of −15.16, Table 1). Increased cod spawning biomass was associated with lower recruitment and increased bottom temperatures were associated with higher recruitment. Neither the distributional extent or the latitude of the centroid of abundance of Tanner crab was better explained by including environmental variables, but the longitudes of the centroid of abundance were significantly better explained by including SST and cod (ΔAICc of −15.27; Table 1). Cod was the strongest predictor of changes in longitude; when cod biomass was high, Tanner crab were distributed farther offshore.

The best model for red king crab recruitment included ice cover and the AO. The change in AICc observed by adding these variables was small (ΔAICc of −0.41; Table 1) and did not exceed the 2-point threshold used to identify "significance" in model selection via AICc (Burnham and Anderson, 2002). Ice cover was negatively related to recruitment; increases in the AO were associated with increased recruitment. The distributional extent and the latitudes and longitudes of the centroids of abundance for red king crab were all better explained by including environmental variables. SST improved the fit to distributional extent the most (ΔAICc −6.39), with higher SSTs associated with larger distributions. Ice cover and the AO significantly improved the explanation of variability in the latitude of the centroid of abundance (ΔAICc = −12.71); red king crab were observed at higher latitudes when less ice was present and the AO was low. Bottom temperature and cod spawning biomass improved the fits to the longitude of the centroids of abundance (ΔAICc = −2.48); when temperatures were higher and cod biomass was lower, red king crab expanded westward onto the shelf.

LOOCV showed that the fit did not change drastically for models for which inclusion of an environmental variable improved performance (Supplementary Figure S2). Removing one point for the model describing the longitudinal component of the centroid of abundance for snow crab resulted in large changes in the fit, which suggests that caution is warranted in its interpretation. The recruitment models produce very similar fits to the data, regardless of which point was removed from the analysis in LOOCV (Figure 6; see Supplementary Table S1 for a summary of best models).

Projections

Projections of snow crab recruitment using the best fit model (ice cover + AO) had similar character to historical snow crab recruitment under the optimistic warming scenario—periods of relatively low recruitment punctuated by larger year classes (Figure 6). However, under the more pessimistic warming scenario, the large recruitments gradually disappeared, particularly past 2040. Declines in ice cover are the primary driver of the projected decrease in snow crab productivity under warming.

Table 1. Change in AICc for regressions fit to recruitment and spawner estimates, the extent distribution of each species, and the latitude and longitude of the centroids of abundance.

	Recruitment			Distribution			Latitude			Longitude		
Ice_cover + Cod + Aleutian.Low	0.80	-1.54	3.93	6.16	5.62	-0.80	0.96	7.66	-11.33	3.18	-8.97	3.14
SST + Cod + Aleutian.Low	1.19	-4.67	3.72	6.71	6.31	-2.07	-0.37	7.66	-1.93	3.02	-10.41	3.81
Bottom_temp + Cod + Aleutian.Low	1.78	-12.10	4.49	7.23	6.25	-6.39	2.29	7.62	0.98	2.48	-6.46	-0.82
Ice_cover + Cod + Arctic_oscillation	-4.74	0.45	0.62	7.01	8.06	-0.59	-1.39	7.91	-11.40	-5.65	-8.18	3.21
SST + Cod + Arctic_oscillation	-1.70	-4.14	2.29	7.65	8.26	-2.06	-5.15	7.82	-3.51	-6.84	-10.65	3.74
Bottom_temp + Cod + Arctic_oscillation	-3.94	-12.64	2.85	7.99	8.28	2.38	-0.25	7.92	0.93	-6.61	-5.92	0.55
Ice_cover + Cod + PDO	-3.50	0.45	4.08	6.94	8.27	-0.60	1.92	6.78	-10.17	4.18	-9.48	3.32
SST + Cod + PDO	0.66	-4.30	4.11	7.33	8.40	-2.09	-0.05	6.45	-3.07	3.75	-11.49	4.04
Bottom_temp + Cod + PDO	0.22	-13.17	4.85	7.50	8.40	2.16	2.20	6.40	-0.93	2.97	-8.32	0.30
Ice_cover + Cod + Alaskan_index	3.13	0.41	3.48	7.02	7.98	-0.57	3.28	7.02	-9.44	0.66	-9.97	2.55
SST + Cod + Alaskan_index	5.18	-4.75	3.40	7.49	8.38	-2.09	1.21	7.20	-0.16	0.61	-12.79	2.80
Bottom_temp + Cod + Alaskan_index	4.05	-13.75	4.10	7.71	8.39	2.17	4.08	6.97	2.92	0.40	-6.92	0.46
Ice_cover + Cod	2.46	-2.55	0.85	3.98	5.21	-3.67	0.61	4.84	-12.01	1.19	-10.96	0.30
SST + Cod	3.50	-7.15	0.85	4.57	5.33	-5.15	-1.71	4.74	-3.26	0.73	-13.05	0.95
Bottom_temp + Cod	1.61	-15.16	1.59	4.92	5.33	-0.72	1.59	4.84	-0.12	-0.09	-8.69	-2.48
Ice_cover + Aleutian.Low	-1.63	4.71	3.73	4.12	2.76	-1.83	0.49	5.11	-11.14	3.68	3.28	5.36
SST + Aleutian.Low	-0.18	1.88	2.17	4.52	3.28	-3.60	-0.04	4.96	-3.87	3.69	3.24	5.35
Bottom_temp + Aleutian.Low	-0.09	-12.27	3.62	4.72	3.22	2.51	0.96	5.16	-1.81	3.64	3.29	3.89
Ice_cover + Arctic_oscillation	-7.73	5.35	-0.41	4.72	5.11	-2.21	-3.57	5.13	-12.71	-7.78	1.90	3.87
SST + Arctic_oscillation	-4.04	1.89	0.08	5.09	5.17	-1.83	-6.48	4.94	-6.12	-8.37	1.30	3.89
Bottom_temp + Arctic_oscillation	-6.49	-12.30	1.12	5.26	5.19	2.02	-2.86	5.17	-2.12	-8.34	2.04	2.75
Ice_cover + PDO	-5.21	5.01	3.66	4.48	5.22	-1.91	1.56	3.93	-9.83	4.98	2.91	5.35
SST + PDO	0.07	-0.35	2.75	4.67	5.31	-3.70	0.81	3.51	-4.76	5.02	2.99	5.28
Bottom_temp + PDO	-0.97	-14.30	4.08	4.70	5.31	2.45	1.51	4.25	-3.48	4.70	2.96	4.08
Ice_cover + Alaskan_index	0.10	5.35	3.66	4.66	4.94	-1.79	3.41	4.44	-8.35	1.93	4.37	4.48
SST + Alaskan_index	2.63	0.69	2.60	4.92	5.29	-3.63	2.47	4.46	-1.44	2.28	3.91	4.08
Bottom_temp + Alaskan_index	1.37	-13.09	3.74	4.97	5.29	2.36	3.56	4.37	0.50	2.68	4.40	4.06
Ice_cover	-0.28	2.56	1.16	1.92	2.44	-4.59	1.09	2.46	-10.85	2.55	2.32	2.55
SST	1.10	-0.90	-0.02	2.30	2.52	-6.39	-0.11	2.23	-4.24	2.49	2.07	2.54
Bottom_temp	-0.82	-14.13	1.27	2.46	2.52	-0.27	1.28	2.51	-2.26	1.99	2.35	1.37
Cod	1.79	-4.32	1.33	2.37	2.57	-2.22	1.38	2.02	2.57	-0.66	-8.02	-1.33
Aleutian.Low	1.15	2.11	2.70	2.27	0.54	1.89	-1.70	2.35	-2.23	0.91	0.49	2.57
Arctic_oscillation	-5.40	2.60	0.61	2.56	2.42	2.20	-4.32	2.43	0.04	-10.54	-0.61	1.08
PDO	1.04	2.23	2.73	1.88	2.57	1.66	-1.13	1.87	-4.39	2.20	0.18	2.54
Alaskan_index	2.43	2.57	1.44	2.15	2.49	1.02	1.08	1.66	0.79	-0.12	2.34	1.80

Colours indicate a model for which the AICc was lower for a model that incorporated environmental factors. Darker colours represent higher support for a given model relative to the base model. Colour by species is consistent with other figures: blue = snow, green = Tanner, red = red king. Change in AICc is relative to a Ricker curve with only spawning biomass for the "recruitment" column and relative to a linear model with slope equal to zero for all other columns.
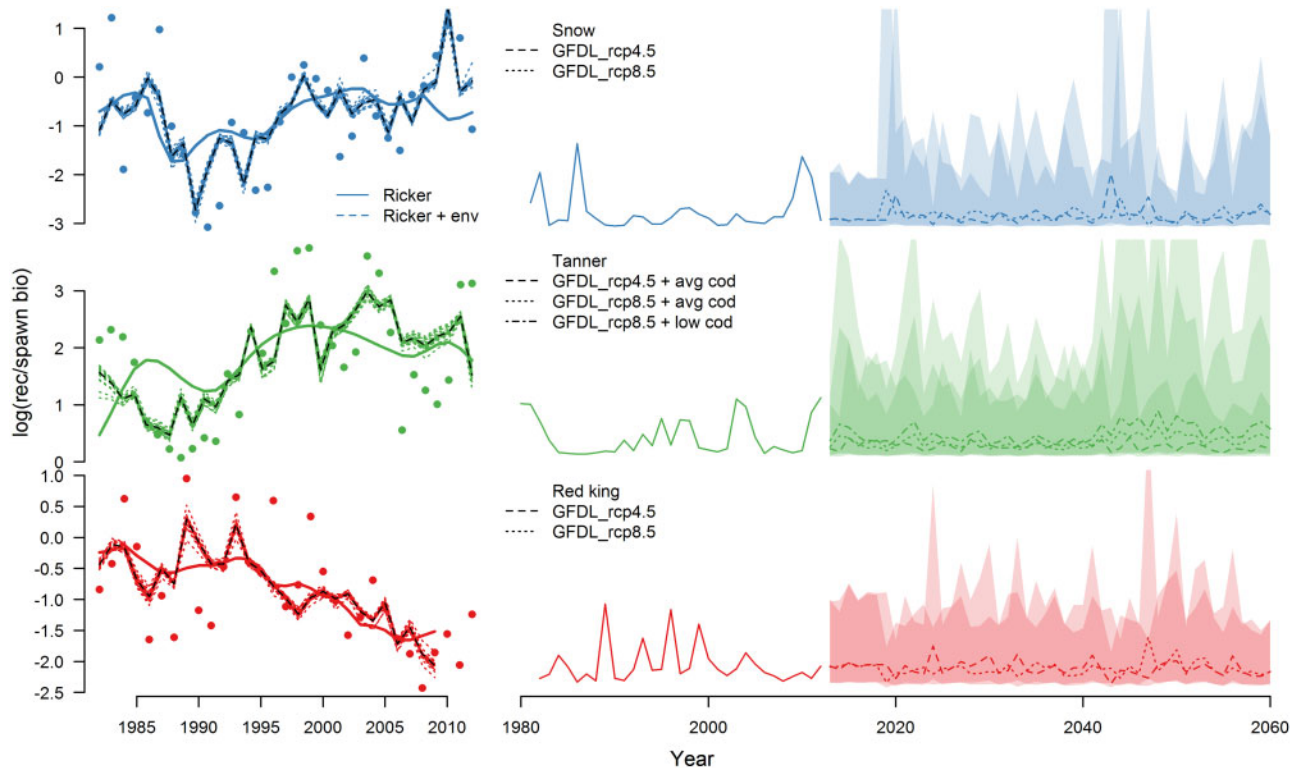
Figure 6. Scatter plot of log(recruits per spawner biomass), fits of Ricker curve with (dashed line) and without (solid line) environmental indices (left column). Dotted lines around the dashed line represent fits to the data via iterations of LOOCV. Time series of historical estimated recruitment (solid line) and projections of recruitment based on fitted models (right column). The fitted curves in the left column and projection in the right column are from the model with the lowest AICc. Shaded areas in the projection indicate the 95% prediction intervals.

The AO most strongly determined the centroids of abundance for snow crab, and this is largely because of its relationship to recruitment. Recruitment generally occurs on the Northeast portion of the Bering Sea shelf, so, when large recruitment events occur, the latitudes and longitudes associated with the centroid of abundance shift that direction. Aspects of this relationship can be seen in the relationship between changes in latitude and longitude of the centroids of abundance with bottom temperature, SST, and cod (Table 1). Historically, when bottom temperatures were low, the centroid of abundance was farther east; similarly, when SST was low, the centroid of abundance was farther south. Given these relationships, the centroid of abundance would be expected to move north and west under warming scenarios, with larger changes associated with more warming (Figure 7).

Little difference in Tanner crab recruitment was predicted among scenarios for the first 20 years of projection (to year 2040), but after 2040 models with higher warming and fewer cod predicted increased productivity (Figure 6). The time series of the longitude of the centroid of abundance was the only aspect of Tanner crab distribution that was better fit by including an environmental variable. Cod was strongly related to the east/west distribution of the stock, but SST also improved fits (Table 1). Similar to Tanner crab recruitment, differences among scenarios in longitude of the centroid appeared after 2040, with models in which there was more warming and less cod resulting in farther movement to the west (Figure 7).

Red king crab recruitment was relatively stable over the projection period; ice cover was negatively associated with recruitment, so increasing temperatures resulted in small increases in productivity (Figure 6). The distributional extent of red king crab decreased under warming scenarios when projected with SST. Projected centroids of abundance moved farther east and north under increased warming and lower cod scenarios, driven by changes in bottom temperature (longitude) and ice cover (latitude) (Figure 7).

Discussion

We linked recruitment and distributional dynamics of the largest commercially exploited crab stocks in the Bering Sea to environmental variables that are expected to change under a warming climate. Some of these relationships have not been reported in the literature (e.g. the AO and snow crab); others reaffirm previously observed relationships with updated data (e.g. bottom temperature and red king crab distribution). Other identified relationships update hypotheses on crab population dynamics like the "environmental ratchet" hypothesis for snow crab [the centroid of abundance for snow crab moved sharply south almost immediately after Orensanz *et al.* (2004) published their paper, suggesting the changes in distribution were related to recruitment dynamics]. LOOCV showed that the identified relationships were relatively robust to the removal of individual observations. These stocks currently occupy roughly complementary areas in the eastern Bering Sea, but our projections of productivity and distribution of each of these stocks based on observed relationships and GCMs suggest that their productivity and distribution may change in the future.

Changes in distribution and productivity could have important implications for the management of these stocks. Currently, each of these stocks is assessed and managed jointly by the State of Alaska and the National Oceanic and Atmospheric Administration. In an abbreviated description of this process, an
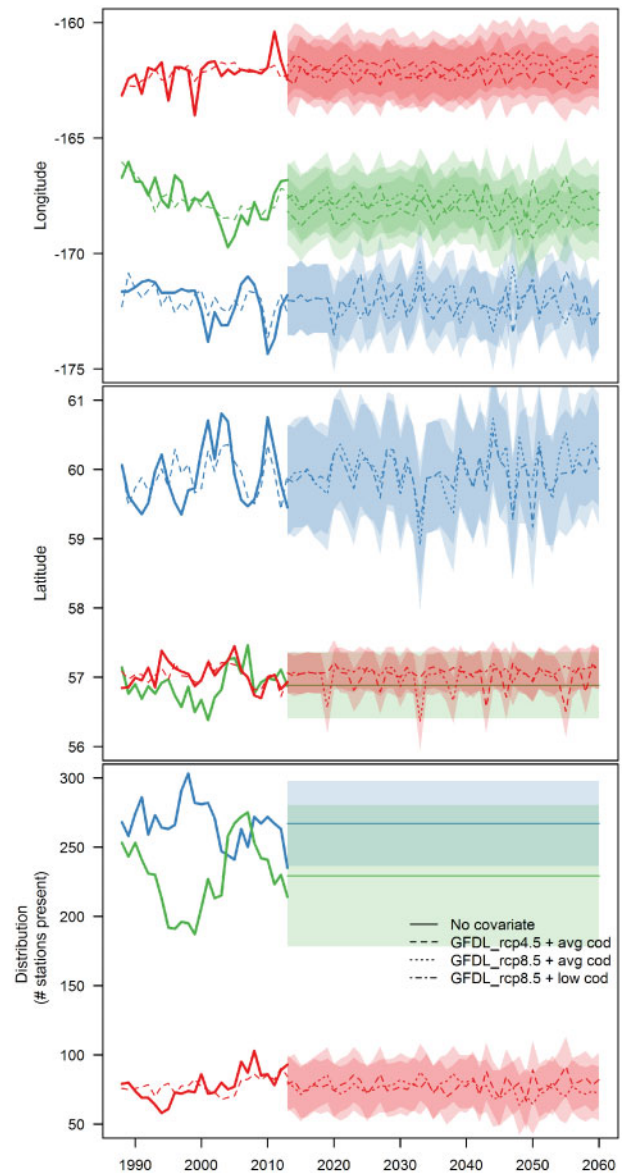

Figure 7. Changes in distributional extent represented as the number of stations at which a given species were observed (bottom) and centroids of abundance over time in terms of latitude (middle) and longitude (top). Colours represent species and are consistent with other figures. Solid lines in the historical period are the observations, and dashed lines laid over the observations are best fit models incorporating environmental indices (chosen by change in AICc). Projection period (from mid-2010s onward) used the 4.5 and 8.5 RCP scenarios. For stocks in which cod biomass was a significant predictor, a low and average cod biomass was projected forward under the 8.5 emissions scenario. Shaded areas are 95% prediction intervals.

assessment is performed yearly for each stock that incorporates available new data (e.g. catch and scientific survey biomasses and length composition data). A total allowable catch is calculated using the assessment output (i.e. an estimated biomass, fishing mortality, and biomass reference points) and a sloped harvest control rule. The State of Alaska then sets catch limits for the year within this constraint, and then, the allowable catch is then

divided among quota holders and bycatch fisheries to be caught in the coming fishing season. Fishing mortality reference points are calculated as the fishing mortality that would reduce the spawning biomass per recruit to 35% of unfished levels ($F_{35\%}$; see Clark, 1993). Biomass reference points used in the analysis are based on the product of the spawning biomass per recruit resulting from fishing at $F_{35\%}$ and the average recruitment over a period of time considered to represent the current environmental conditions. [See Szuwalski (2019) for a more complete description of this process.]

Changes in productivity (as seen through recruitment) will directly influence the calculation of biomass reference points. Historically, the time period of recruitment used to calculate an average productivity began shortly after the regime shift in the North Pacific (1976/1977; Overland *et al.*, 2008). Depending on how changes in what appear to be important environmental variables in our analysis occur (as opposed to the projections), changes in the way the average productivity is calculated might be required. It is unclear at what point changes should occur, but, based on the projections described here, the largest projected changes in productivity occur after 2040. The calculation of fishing mortality reference points is not directly influenced by changes in recruitment; however, it is possible that the population processes (e.g. natural mortality, selectivity, growth) that determine $F_{35\%}$ will change over this period of time as well, and management may need to respond to these changes (Szuwalski and Hollowed, 2016). Estimating time variation in the processes that that determine $F_{35\%}$ is difficult with commonly available data for assessment (Johnson *et al.*, 2015). Further complicating the issue, the data available for assessment are often fit better when time variation in any process is estimated, but, if the wrong process is allowed to vary, the resulting reference points can be biased (Szuwalski, 2019). The most reliable way of understanding changes in these processes involves directed field studies (e.g. Somerton *et al.*, 2013), but these can be expensive and time-consuming.

Changes in the distribution of the stocks can also influence other aspects of these fisheries. The current assessment process assumes that these populations are fully contained within the surveyed range. However, it is known that a fraction of the population of snow crab is outside of the surveyed area (Zacher *et al.*, 2019) and, given our projections, this fraction may increase in the future. Changes in distribution of the stocks will also influence the fishery itself. Relatively few processors and ports currently service the fleets fishing for these crab and the ones that do are located primarily in southern Alaska. Shifts in distributions could result in increases in the distance to fishing grounds from current ports and concomitant increases in fuel costs. Although snow crab are more abundant, red king crab are more valuable, so changes in relative productivity among the species could also have impacts on market timing and supply chain dynamics.

Some models presented had significant but relatively small improvements over models with no environmental variables, so these should be approached with caution. Although LOOCV indicated that most observed relationship was relatively robust to the exclusion of individual data points, linking productivity to environmental variables has been consistently shown to be a problematic pursuit (e.g. Myers, 1998). Relationships between productivity and environmental variables for stocks in this analysis appear to have broken down over time [e.g. snow crab recruitment and the PDO (Szuwalski and Punt, 2013) and red king crab

and the Aleutian Low (Zheng and Kruse, 2006)]. Furthermore, including environmental variables in management strategies often provides little benefit to management unless the mechanisms are well known (Punt *et al.*, 2014). So, although it is tempting to hypothesize about mechanisms behind the observed relationships, we instead propose further spatiotemporal studies before attempting to identify mechanisms. Analyses such as ours operate with aggregate data streams out of necessity, but analytical techniques are emerging that allow for performing similar analyses in both space and time (Thorson, *et al.*, 2016; Cao *et al.*, 2020).

Other factors not considered here may also influence productivity and distribution. For example, red king crab are known to prefer rocky habitat, but our analyses do not include habitat. Consequently, realized changes in red king crab distribution may be different than our projections. Ocean acidification is another variable that is known to impact crab larvae in the area for some species (e.g. Long *et al.*, 2019) but has not been incorporated into the projections here. Long-term time series of pH are not available for the habitats in which crab are found (though efforts are underway to produce these; e.g. Pilcher *et al.*, 2019), so it is not possible to develop a predictive model for the impact of pH on crab distribution or productivity in the way we have done here. Projections based on laboratory studies on the impacts of OA and Bering Sea crab suggest that the productivity of Tanner crab and red king crab will be negatively impacted (Punt *et al.*, 2014, 2016).

Other covariates that vary over space and time like habitat, dissolved oxygen, and salinity could be incorporated into future spatiotemporal analyses. Our projections may also be somewhat conservative based on the use of the GFDL-ESM2M model, which projects somewhat less drastic changes under increased emissions scenarios than other GCMs (Hermann *et al.*, 2019). Incorporating ensemble modelling techniques in future analyses across GCMs and population dynamics models could better account for among-model uncertainty (Hollowed *et al.*, 2020).

In spite of potential limitations, aggregate analyses such as those presented here can be useful in two ways. First, they can be useful for identifying environmental variables important in determining prevailing environmental conditions for a given stock. The assessment and management of these stocks are performed using spatially aggregated assessments and require a time period to be defined for use in defining management targets. Time periods over which the variables identified as important predictors of productivity can be identified by looking for stationary sections of these time series. Aggregate analyses can also be used as springboards to direct spatiotemporal analyses exploring mechanistic relationships between distribution, productivity, and environment. Ultimately, we hope that this project can serve as a piece in the puzzle of determining the appropriate model complexity for managing the changing crab stocks of the Bering Sea.

Supplementary data

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

Data availability

Recruitment and spawning biomass estimates are available in the assessments published by the North Pacific Fisheries Management Council (www.npfmc.org). Historical indices of environmental variation are available at the Bering Sea Ecosystem and Climate portal (beringclimate.noaa.gov). Spatial survey data

can be accessed with the R package "FishData". Projections of local and large-scale indices of environmental variation can be requested from KH and JL.

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