

Recent shifts in northern Bering Sea snow crab (*Chionoecetes opilio*) size structure and the potential role of climate-mediated range contraction

Erin J. Fedewa^{a,*}, Tyler M. Jackson^b, Jon I. Richar^a, Jennifer L. Gardner^a, Michael A. Litzow^a

^a Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 301 Research Court, Kodiak, AK, 99615, USA

^b Alaska Department of Fish and Game, Commercial Fisheries Division, 351 Research Court, Kodiak, AK, 99615, USA



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ABSTRACT

Recent historic lows in sea ice and cold pool extent in the Bering Sea have been linked to large-scale biogeographic shifts in many demersal taxa. Snow crab (*Chionoecetes opilio*) are associated with the cold pool and thus may be especially prone to northward range contraction with continued warming. Data from the 1988–2019 National Marine Fisheries Service eastern Bering Sea (EBS) bottom trawl surveys were used to examine the effect of climate warming on snow crab thermal habitat use and spatial distributions. The northern Bering Sea (NBS) was also surveyed in 2010 and 2017–2019, allowing us to examine NBS snow crab demographic structure relative to potential climate-driven range contraction into the NBS. Across the time series, trends in temperatures occupied by snow crab were tightly coupled with average bottom temperatures in the EBS despite extreme temperatures in 2018–2019 that exceeded cold-water thermal preferences of juvenile snow crab. Furthermore, we found that increased temperatures and a reduced, more northerly cold pool extent resulted in a smaller area occupied by snow crab across different ontogenetic stages, although there was no evidence for a northward shift in centers of distribution within the EBS. These findings suggest that the spatial extent and average temperature of snow crab distribution are likely constrained by the availability of cold water habitat in the EBS, and dramatic declines in juvenile snow crab abundance observed in 2019 may be attributed to potential direct or indirect temperature effects on survival of highly stenothermic early benthic stages of snow crab. Despite limited support for a directional range shift, survey abundance estimates indicated a ~600% increase in abundance of larger size classes of male snow crab (≥ 61 mm carapace width) in the NBS between 2018 and 2019. Substantial shifts in juvenile abundances and NBS snow crab size structure in 2019 may have important management implications for the stock. While the increase in NBS mature male biomass may suggest the potential for a commercial fishery in more northern latitudes, concurrent declines in juvenile abundance suggest caution concerning the sustainability of the stock with continued warming.

1. Introduction

Snow crab (*Chionoecetes opilio*) are widely distributed across subpolar and Arctic regions, supporting commercial fisheries in both the North Pacific and North Atlantic. The southeastern Bering Sea (EBS) represents the southern extent of snow crab range in the North Pacific and supports one of the largest crab fisheries in the world, with annual ex-vessel revenue peaking at \$174 million in the past decade (Garber-Yonts and Lee, 2018). The EBS snow crab fishery is male-only and biological reference points for fishery management are determined using mature male biomass estimated from a length-structured population dynamics model (Szuwalski, 2019). Although snow crab dominate the benthic

invertebrate biomass in the northern Bering Sea (NBS), cold temperatures have historically prevented males in the region from reaching commercially-preferred sizes (Kolts et al., 2015), and seasonal sea ice has limited access to northern fishing grounds during the winter fishery. Sea ice dynamics strongly influence ecosystem structure in the Bering Sea and drive distinctly different biological processes and community assemblages between EBS and NBS shelf habitats. The NBS, delineated by a 59–60°N transition zone, has been characterized by the presence of sea ice from October to late-June and very cold bottom temperatures (<1 °C), whereas sea ice in the EBS is typically only present from December to mid-May (Stabeno et al., 2012a, 2012b). Strong pelagic-benthic coupling supports high benthic production and large

* Corresponding author.

E-mail address: erin.fedewa@noaa.gov (E.J. Fedewa).

invertebrate communities in the NBS (Grebmeier et al., 1988, 1989), while pelagic processes dominate in the EBS, sustaining high gadid, flatfish and forage fish biomass (Stevenson and Lauth, 2012).

The spatial extent of seasonal ice cover and the timing of ice retreat also strongly influence spatial distributions of groundfish and crab species in the Bering Sea (Spencer, 2008; Mueter and Litzow, 2008). In the middle shelf domain, between the 50 m and 100 m isobaths, spring ice melt sets up a two-layer summer stratification characterized by a warm surface layer and the formation of a cold pool of bottom water $<2^{\circ}\text{C}$ (Stabeno et al., 2001). Arctic species such as snow crab concentrate on the middle shelf in this cold pool, whereas many commercially important groundfish species are restricted to warmer waters (Kotwicki and Lauth, 2013). As such, the cold pool can at times act as a thermal barrier to major groundfish predators such as Pacific cod (*Gadus macrocephalus*) and provides a predator refuge for juvenile snow crab (Orensanz et al., 2004). In the past decade, however, major ecosystem reorganization has led to a borealization in Arctic ecosystems, and north-south boundaries delineating Arctic and sub-arctic ecosystems have begun to shift (Grebmeier et al., 2006; Grebmeier, 2012; Fosheim et al., 2015; Frainer et al., 2017). Anomalous conditions have been reported in the EBS in recent years, and 2018 marked the smallest cold pool and lowest sea-ice extent on record (Stabeno and Bell, 2019; Thomas et al., 2019; Duffy-Anderson et al., 2019). Similarly, unprecedented warming from 2017 to 2019 in the NBS suggests a sudden and dramatic ecosystem transformation in the Pacific Arctic (Huntington et al., 2020). Comparisons with climate model simulations run under pre-industrial conditions indicate that these temperature anomalies would have been impossible without anthropogenic radiative forcing (Walsh et al., 2018). Recent large-scale distribution shifts in walleye pollock (*Gadus chalcogrammus*) and Pacific cod have been attributed to northward migrations into the NBS as a potential response to a retreating cold pool (Stevenson and Lauth, 2019; Spies et al., 2019). Similar snow crab poleward distribution shifts into the NBS have not yet been documented, and may be difficult to detect due to the large biomass of snow crab historically present in northern latitudes and relatively few observations available in the NBS. However, high sensitivity to climate change (Spencer et al., 2019) and predicted shifts in snow crab biomass linked to climate-driven changes in benthic production (Lovvorn et al., 2016) necessitate the integration of snow crab spatial and demographic studies across Bering Sea regions to elucidate population-level responses to shifting environmental conditions.

Spatial patterns in snow crab distribution are determined largely by ontogenetic migrations linked to size- and sex-specific thermal requirements. Immature snow crab concentrate in colder, shallow waters of the NBS and EBS middle shelves, and temperature is an important determinant of spatial structure within each region (Murphy et al., 2010; Kols et al., 2015). Likewise, primiparous female snow crab appear to track near-bottom temperature during a northeast to southwest ontogenetic migration to warmer waters near the shelf break (Ernst et al., 2005; Parada et al., 2010). As environmental conditions rapidly change in the Bering Sea, suitable temperatures could begin to disappear for snow crab in the EBS, forcing populations to relocate in an effort to maintain thermal optima. Following a warm stanza in the late 1970s, EBS snow crab centers of distribution shifted northward towards St. Matthew Island (Zheng et al., 2001; Orensanz et al., 2004); however, the response of snow crab to continued warming and loss of sea ice in the Bering Sea is uncertain. Projected climate change in the Bering Sea is expected to trigger a northward range contraction in snow crab driven by thermal habitat requirements (Morley et al., 2018; Murphy, 2020), suggesting that the NBS could become relatively more important as suitable habitat for snow crab as temperatures continue to increase. North Pacific snow crab comprise a single population with a contiguous distribution (Albrecht et al., 2014), and connectivity between the EBS and NBS is likely uninhibited, as there are no significant bathymetric obstacles to migration or oceanographic obstacles to larval dispersal. As such, we hypothesize that as bottom temperatures increase and the cold

pool shrinks, EBS snow crab will be unable to maintain thermal preferences and the population range will contract northward into the NBS.

Changing climatic conditions can also influence demographic processes in species such as snow crab that occupy large geographic ranges and thermal habitats. Snow crab biomass in the NBS is dominated by immature crab, with a historically small mature population and few individuals exceeding 60 mm carapace width (Chilton et al., 2011; Lang et al., 2018). The NBS region may therefore serve as a larval sink due to low predation pressure and localized currents that support larval retention (Parada et al., 2010; Kolts et al., 2015; Lovvorn et al., 2015). Latitudinal variation in snow crab mean body size and size at maturity have been explained in part by year-round colder bottom temperatures in more northerly latitudes (Otto, 1998; Orensanz et al., 2007), and consequently, latitudinal clines in snow crab demographics have the potential to shift in response to climate change. While increased snow crab growth potential, molt frequency and size at maturation may be attributed to warmer temperatures (Dawe et al., 2012; Yamamoto et al., 2015), more immediate population responses could occur as snow crab from the EBS track thermal preferences northward. Likewise, the geographic range of snow crab could contract north if warming in the Bering Sea shortens north-to-south ontogenetic migration patterns driven by thermal gradients (Parada et al., 2010). These responses, evident as an increase in both overall abundance and the proportion of large snow crab in the NBS, may indicate a decline in the magnitude of variation in Bering Sea snow crab demographics as the NBS transitions from an Arctic to a subarctic system.

The National Marine Fisheries Service (NMFS) annual EBS bottom trawl survey of groundfish and invertebrate fauna offers the means to explore patterns in spatial distributions and temperatures occupied by snow crab in the EBS under both cold (1995, 1997–1999, 2007–2013) and warm (2001–2005, 2014–2019) periods (Stabeno et al., 2012b; Stabeno and Bell, 2019). The NMFS survey was also expanded to include the NBS during years that encompass both cold (2010) and warm (2017–2019) conditions. The goal of the current study is to evaluate the hypothesis that increased temperatures experienced by snow crab and climate-driven northward range contraction in the EBS will result in changing demographic structure of NBS snow crab. Our first objective is to compare snow crab temperatures of occupancy (mean bottom temperature weighted by CPUE) with bottom temperatures in the EBS, allowing us to determine the extent to which temperatures experienced by snow crab have shifted relative to the range of temperatures potentially available to them in the EBS. We then assess the importance of average bottom temperatures, cold pool extent, and cold pool latitudinal centers as drivers of snow crab centers of distribution and spatial extent. Finally, we compare abundance and size structure of NBS snow crab across years to examine evidence for EBS snow crab range contraction into the NBS.

2. Material and methods

2.1. Survey sampling

The EBS bottom trawl survey is conducted from approximately May through August and utilizes a systematic grid design (20×20 nm grids) with 376 stations (Fig. 1). Due to changes in survey extent and stations sampled prior to 1988, catch data for our analyses were limited to standardized survey years (1988–2019). In 2010, 2017 and 2019, the EBS trawl survey was expanded to incorporate 145 standardized stations in the NBS. The EBS survey was also extended northward in 2018, however only 49 stations (30×30 nm grids) were sampled in the NBS, encompassing the Bering Strait region to St. Lawrence Island. The EBS survey grid is divided into three sampling strata representing 1) the standard survey grid stations, and high-density multi-tow stations (i.e. center and corner stations) around 2) the Pribilof Islands and 3) St. Matthew Island. The NBS grid contains a smaller number of stations and thus only consists of a single stratum.

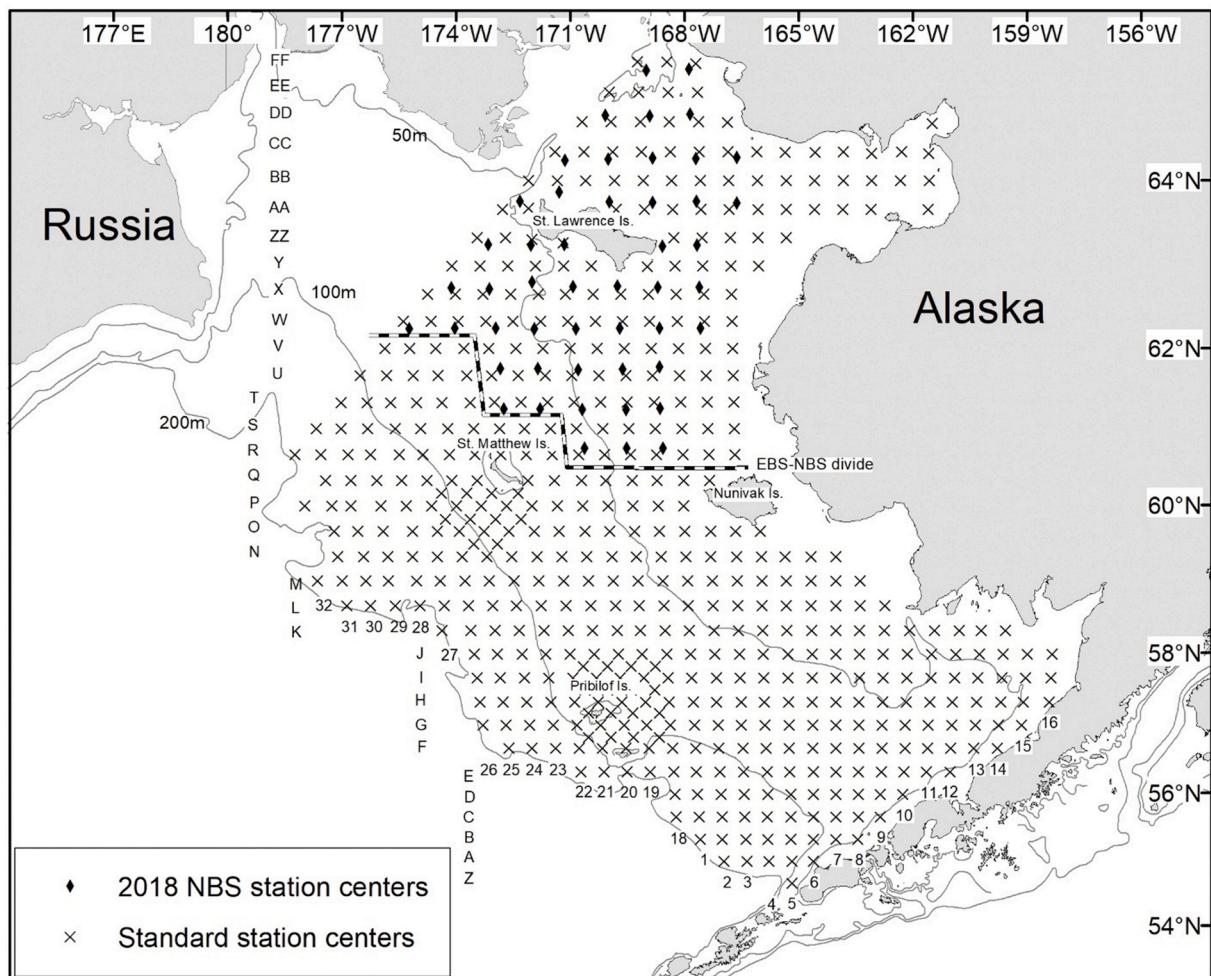


Fig. 1. Standard survey area for the National Marine Fisheries Service eastern Bering Sea (1988–2019) and northern Bering Sea (2010, 2017–2019) summer bottom trawl surveys. “X” denotes standard station centers, while “◆” denotes northern Bering Sea (NBS) station centers in 2018 (30×30 nautical mile grid squares). The dashed line labeled EBS-NBS divide is the boundary between the two survey areas. In 2018, the AFSC Rapid Response survey was unable to sample the nearshore areas of the open coast and Norton Sound.

Trawl gear, deployment and operations followed NMFS bottom trawl standards (Stauffer, 2004) and all tows were conducted for 0.5 h using a standard 83–112 Eastern otter trawl employing an 83 ft (25.3 m) headrope and a 112 ft (34.1 m) footrope. Bottom water temperatures were collected at each station using a Sea-Bird SBE-39 datalogger (Sea-Bird Electronics Inc., Bellevue, WA) attached to the headrope of the net. Net height and width during each tow were measured in 1-sec intervals with net mensuration equipment (Marport sensors), and continuous contact of the center of the footrope with the bottom was determined using a bottom contact sensor (Stauffer, 2004). Snow crab biological data collected at each station included total catch weight, carapace width (CW) measurements (± 0.1 mm), shell condition classification, chela height measurements for male snow crab, and clutch assessment for female snow crab (Jadamec et al., 1999; Zacher et al., 2020). Catch data for each station were standardized to catch per unit effort (CPUE; individuals nm^{-2}) by dividing the total number of snow crab caught in each 1 mm CW bin by area-swept effort (average net width multiplied by distance towed). Abundance of crab within each stratum (N_s) was estimated by multiplying the mean CPUE of each size bin by the total area of the stratum (A_s). Annual abundance estimates within each region (N_r) were computed as the sum of abundance estimates within each stratum weighted by A_s in proportion to the area of the region (A_r). Since the NBS represents a single stratum, A_s is equivalent to A_r .

$$N_r = \sum_{i=1}^n \frac{A_{s_i}}{A_r} N_{s_i} \quad (1)$$

2.2. Eastern Bering Sea environmental variables

Annual environmental indices were developed to describe EBS thermal conditions and cold pool dynamics (Fig. 2). Station bottom temperatures were used to calculate an average bottom temperature index for each year. Missing temperatures across the 32-year time series ($n = 428$ stations; 3.5% of total) were estimated using multiple imputation by chained equations in the R package *mice* (van Buuren and Groothuis-Oudshoorn, 2011). Estimated temperatures were averaged from the distribution of 100 imputed values and the resulting dataset was used for all further analyses. Cold pool spatial extent was computed as the number of EBS stations in each year with a bottom temperature measurement $< 2^\circ\text{C}$, multiplied by the area of a standard survey grid cell (401 nm^2). Cold pool center of distribution was determined by averaging the mid-latitude of EBS survey stations with bottom temperature $< 2^\circ\text{C}$ in a given year. High density strata stations, centered at the corner of each $20 \times 20 \text{ nm}$ grid cell near the Pribilof Islands and St. Matthew Island, were excluded from both cold pool extent and cold pool center of distribution calculations ($n = 28$ stations).

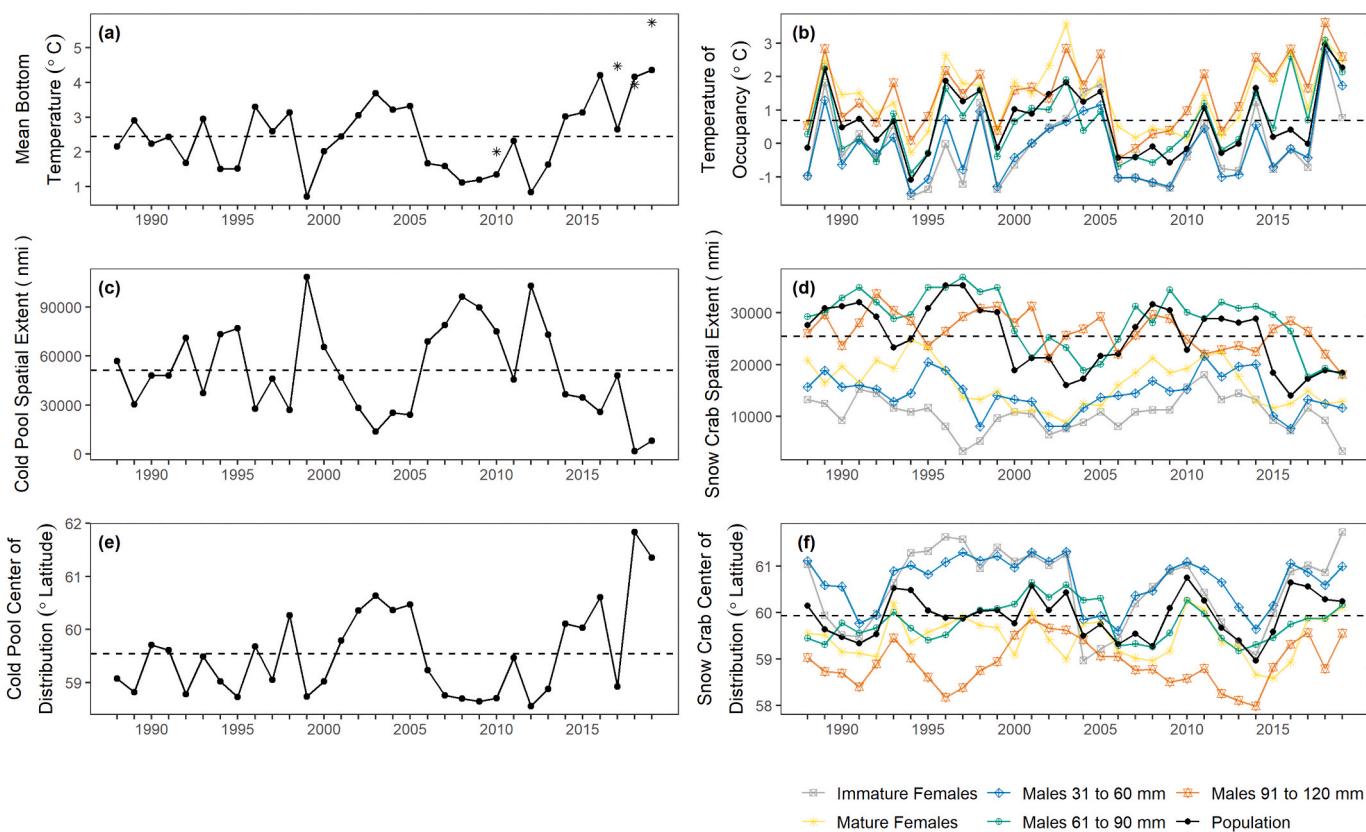


Fig. 2. Eastern Bering Sea environmental and snow crab spatial indices (1988–2019): a) mean bottom temperature ($^{\circ}\text{C}$) with northern Bering Sea mean bottom temperature (*) for 2010 and 2017–2019, b) snow crab temperature of occupancy, c) cold pool spatial extent, d) snow crab spatial extent, e) cold pool center of distribution, and f) snow crab center of distribution. Bold black lines in panels (b), (d) and (f) denote snow crab population means, while transparent colored lines denote snow crab size and sex categories of immature females (□), mature females (*), 31–60 mm carapace width (CW) males (◊), 61–90 mm CW males (○), and 91–120 mm CW males (■). Dashed horizontal lines indicate environmental and population means for each time series.

2.3. Eastern Bering Sea snow crab spatial indices

To examine thermal requirements and spatial structure across multiple snow crab life history stages, temperature of occupancy and spatial distribution indices were estimated across several ontogenetic stages for male and female snow crab. Morphometric maturity in male snow crab is estimated with a distribution-based cutline approach that utilizes an allometric relationship between male chela height and carapace width (Lang et al., 2018; Zacher et al., 2020). Male snow crab reach the terminal molt (i.e. molt to morphometric maturity) over a large range of sizes (Conan and Comeau, 1986; Comeau and Conan, 1992), and size at maturity has been shown to vary across regions and years (Orensanz et al., 2007). Thus, for the purpose of this study, classifying male snow crab in size bins rather than by maturity status was more meaningful in relating findings to a length-based assessment model and size-selective male fishery. Male snow crab were pooled into three biologically-relevant size bins based on individual carapace width: 31–60 mm, 61–90 mm, and 91–120 mm. The NMFS bottom trawl gear samples immature snow crab <30 mm CW with low efficiency (Somerton et al., 2013b; Kotwicki et al., 2017), therefore the 0–30 mm CW category was eliminated from further analyses. The 31–60 mm CW category captures primarily juvenile male snow crab in the EBS, whereas the 61–90 mm CW category identifies males that have begun to reach morphometric maturity, with 78 mm CW delineating legal size in the directed EBS snow crab fishery (NPFMC, 2011). In contrast, size at 50% maturity in the NBS is nearly 30 mm smaller than in the EBS (Zacher et al., 2020) and many NBS males reach morphometric maturity at <60 mm CW (Kolts et al., 2015). The final male size category (91–120 mm) represents the large majority of males that have undergone terminal

molt. This group includes the newshell individuals >101 mm CW that are currently targeted by the EBS fishery, and have been historically absent from the NBS. Female snow crab (≥ 31 mm CW) were classified into immature and mature categories based on abdominal flap morphology rather than by CW.

Snow crab temperature of occupancy was determined for each size-sex category by calculating mean bottom temperature weighted by CPUE at each station. A population-level temperature of occupancy index for the EBS snow crab stock was also calculated by weighting bottom temperatures by cumulative CPUE across all size and sex bins. Temperature of occupancy indices were restricted to stations sampled every year in the time series ($n = 311$). EBS snow crab spatial distribution was described using latitudinal centers of distribution and estimates of the area occupied by the stock. To calculate centers of distribution (COD_{lat}) for each survey year, latitude was weighted by CPUE at each station ($CPUE_i$) for a given size-sex category and divided by the cumulative CPUE within each year:

$$COD_{lat} = \frac{\sum_i^n lat_i \cdot CPUE_i}{\sum_i^n CPUE_i} \quad (2)$$

To determine the area occupied by snow crab in each year, we estimated the minimum area containing 95% of the cumulative CPUE for each size-sex category as the number of stations multiplied by the survey station grid area (Swain and Benoit, 2006; Spencer, 2008; Murphy et al., 2010). Only standard 20×20 nm stations common to all survey years were used for spatial extent and center of distribution calculations.

2.4. Data analysis

Relationships between EBS bottom temperature and snow crab temperature of occupancy time series were evaluated using cross-correlation analysis at a maximum lag of 5 years. Because temperature of occupancy indices are derived from EBS bottom temperatures, our statistical approach enabled us to evaluate the strength and direction of the relationship under the hypothesis that weak correlations may suggest that snow crab have the capacity to respond to climate change by occupying preferred-temperature habitats during warming events (e.g. by range redistribution). Correlations were performed in R 3.6.0 (R Core Team, 2019) using the R packages *stats* and *TSA* (Chan and Ripley, 2012). Temporal autocorrelation was accounted for by adjusting the degrees of freedom and deriving correlation coefficients using the modified Chelton method (Pyper and Peterman, 1998).

Generalized least squares and linear mixed-effects models were used to investigate the relative importance of environmental covariates (i.e. average bottom temperature, cold pool extent, and cold pool latitudinal center) as drivers of snow crab centers of distribution and spatial extent response variables across the 32-year EBS time series. Separate models were fit for center of distribution and spatial extent following the approach outline by Zuur et al. (2009). To account for autocorrelation of residuals, models were fit with an auto-regressive correlation structure using restricted maximum likelihood estimation (REML) estimation. Snow crab abundances previously explained a large portion of variation in spatial extent (Murphy et al., 2010), so we included survey abundance estimates across size-sex categories as a fixed effect with no interactions in spatial extent models. The environmental time series were highly inter-correlated ($r = 0.71\text{--}0.88$), precluding a meaningful analysis of the distinct effect on snow crab response variables (Dormann et al., 2007). We therefore used Dynamic Factor Analysis (DFA) to summarize shared variability across environmental covariates. DFA is a dimension-reduction method that is specifically designed for time series applications, and which summarizes variability in multiple time series as a linear combination of common trends, loadings on individual time series, and a variance-covariance error structure (Zuur et al., 2003). We fit single-trend DFA models to the three time-series (average bottom temperature, cold pool extent, and cold pool latitudinal center) using four candidate variance structures (same variances and no covariance, different variances and no covariance, same variances and same covariance, and different variances and covariance) in the R package *MARSS* (Holmes et al., 2018). The best variance structure was identified with Akaike Information Criterion (AIC) model selection, and the trend from that model was used as an explanatory variable in subsequent fixed and mixed-effects modeling. Center of distribution and spatial extent response variables were mean-centered because population-level variation in snow crab spatial indices across male size and female maturity categories (i.e. random intercept effect size) was not of interest for hypothesis testing. We compared full fixed-effects generalized least squares models and mixed effects random slope models with a five-level “size-sex” random effect to account for potential effects of snow crab size and sex on responses. Models were fit with the *gls* and *lme* functions in the R package *nlme* (Pinheiro et al., 2019) and compared using AIC controlled for small sample size (AICc; *MuMin* R package; Barton, 2015) with REML estimation. After selecting the most appropriate model type, full and reduced models were refit to find the optimal fixed components using maximum likelihood (ML) estimation. The final model for each response was then re-fit using REML and model diagnostics were examined for appropriateness of fit.

Northern Bering Sea snow crab size frequency distributions were compared by calculating mean, median and quantiles (25th, 75th and 90th) of male and female size distributions to assess whether shifts in size distributions were consistent with our hypothesis of larger snow crab moving into the NBS in recent years.

3. Results

3.1. Eastern Bering Sea snow crab temperature of occupancy correlations

Snow crab temperatures of occupancy in the EBS were tightly coupled with average bottom temperatures during summer surveys ($r = 0.79\text{--}0.92$, $p < 0.001$) and maximum positive correlations corresponded to a zero-year lag across all five size-sex categories. Patterns in occupied temperatures were approximately 1–2°C below average bottom temperatures in a given year, although large males and mature females consistently occupied temperatures several degrees above the population-level mean (Fig. 2a,b). Following the onset of warming in 2014, immature females and small males (31–60 mm CW) were concentrated in waters below 0°C, whereas mature females and larger males were located in temperature ranges well above the population-level mean. Snow crab occupancy temperatures increased dramatically across all size sex categories in 2018, reaching nearly 2.5°C above the 32-year mean.

3.2. Eastern Bering Sea snow crab spatial distribution trends

Snow crab area occupied and centers of distribution varied considerably across size-sex categories and survey years (Fig. 2). Medium to large males (61–120 mm CW) were consistently more dispersed and occupied more southerly distributions compared to immature females and small males, which were aggregated in northern latitudes of the survey grid. Mature female snow crab occupied a similar latitude to medium sized males, but were highly aggregated. Following the coldest survey year in 1999, increases in area occupied across all size-sex categories from 2003 to 2009 were congruent with increases in cold pool spatial extent and latitudinal center (Fig. 2c–e). Overall, spatial extent of the population has remained well below average since 2015, and for all male size categories, spatial extent in one of the last four years was the lowest on record. Snow crab centers of distribution indicated large deviations in latitude between large males and both immature females and small males in the mid-late 1990s ($>3^\circ$ difference), and again from 2009 to 2012 ($>2.5^\circ$ difference). Latitudinal distributions shifted toward the south across all size-sex categories from 2010 to 2014, but have shifted northward again since 2014.

3.3. Eastern Bering Sea snow crab spatial distribution model results

The best-fit DFA model included an unconstrained error structure. The shared climate trend from this model returned positive loadings on average bottom temperature (0.35) and cold pool center of distribution (0.35), and a negative loading on cold pool extent (-0.29). All three loadings could be distinguished from zero (Fig. S1), indicating strong covariance among the three environmental variables. The shared trend captures the rapid transition to conditions outside the envelope of previous observations during 2014–2019 (Fig. S1).

Generalized least-squares models were selected over mixed-effects models in describing the relationship between the shared environmental trend and spatial extent of snow crab ($\Delta\text{AICc} = 2.2$), as well as center of distribution ($\Delta\text{AICc} = 5.6$), indicating that all size-sex categories underwent a similar response to the environmental time series. The spatial extent of snow crab decreased significantly in relation to warming tracked by the shared environmental trend (Fig. 3; $t = -5.69$, $p < 0.001$), while the fixed effect for snow crab abundance was not significant ($t = 0.53$, $p = 0.6$) and therefore dropped from the final model. Contrary to our hypothesis, the shared environmental trend failed to explain a significant amount of variation in snow crab centers of distribution ($t = 1.85$, $p = 0.07$).

3.4. Northern Bering Sea snow crab demographic structure

Northern Bering Sea snow crab size frequency distributions in 2019

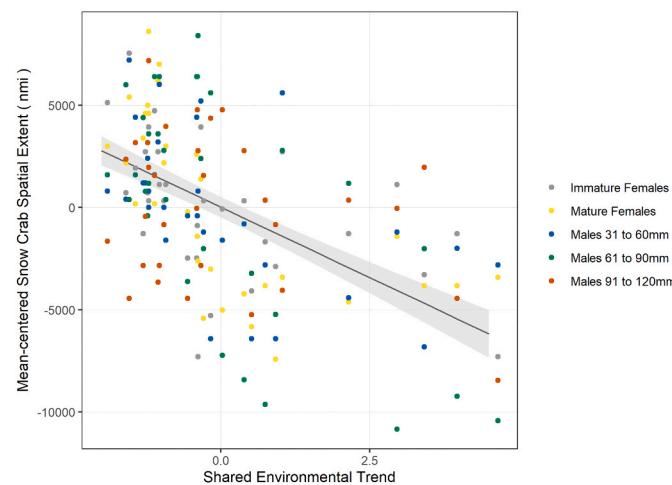


Fig. 3. Spatial extent of eastern Bering Sea snow crab in relation to a shared environmental trend inferred from dynamic factor analysis. The line represents fitted values (\pm SE) from a generalized least squares model and colored observed values correspond to five snow crab size and sex categories.

differed substantially than in 2010, 2017 and 2018 across both male and female populations (Fig. 4). Both the median and 90th percentile size of female snow crab in 2019 were 13% (5 mm) greater than in 2010. Likewise, the median and 90th percentile size of males in 2019 were 25% (10 mm) and 32% (16 mm) greater, respectively, than male sizes in 2010. Trends in total abundance support our hypothesis that shifts in NBS snow crab demographic structure are consistent with an increase in the abundance of large individuals in the NBS. In 2010, estimated abundance of 61–120 mm males in the NBS was approximately 93.1 million crab (95% CI [50.5, 135.6]), with legal size males (≥ 78 mm CW)

constituting < 0.001% of the total male population (Fig. 5). In contrast, 61–120 mm male survey abundance in 2019 was estimated at 625.3 million crabs (95% CI [292.0, 958.6]) and 2.8% of male snow crab in the NBS were of legal size. In addition, the abundance of males >60 mm increased by over 540 million crabs (~600 % increase) from 2018 to 2019. NBS mature female snow crab abundance also increased from 2018 to 2019, although estimates were still well below the 2010 value. Both the EBS and NBS saw dramatic declines in 31–60 mm male snow crab from 2018 to 2019 (Fig. 5). Small male and immature female abundances in the EBS decreased by 89% and 96%, respectively. Likewise, NBS small male and immature female abundances decreased by 48% and 64%, respectively.

4. Discussion

This is the first study to examine responses of snow crab to the unprecedented warming and sea ice decline in the Bering Sea since 2017. We found that temperatures occupied by snow crab in the EBS closely tracked bottom temperatures during this warming event, suggesting that snow crab did not redistribute to cold-water habitats. Limited evidence for spatial avoidance of above-average bottom temperatures from 2017 to 2019 is consistent with the lack of support for a directional shift north in recent years, and climatic conditions did not explain latitudinal trends in snow crab centers of distribution in the EBS. However, model results indicated that the spatial extent of snow crab in the EBS has contracted in response to warmer temperatures and a smaller, more northerly cold pool extent. While this response was uniform across ontogenetic groups, snow crab abundance did not explain trends in spatial extent, suggesting that climate forcing may be more important than density-dependent processes in driving snow crab range contractions. Although we did not detect a range shift northward, the size distribution and abundance of NBS snow crab did show dramatic shifts in 2019 compared to previous years when the NBS was dominated by small, immature snow crab. A

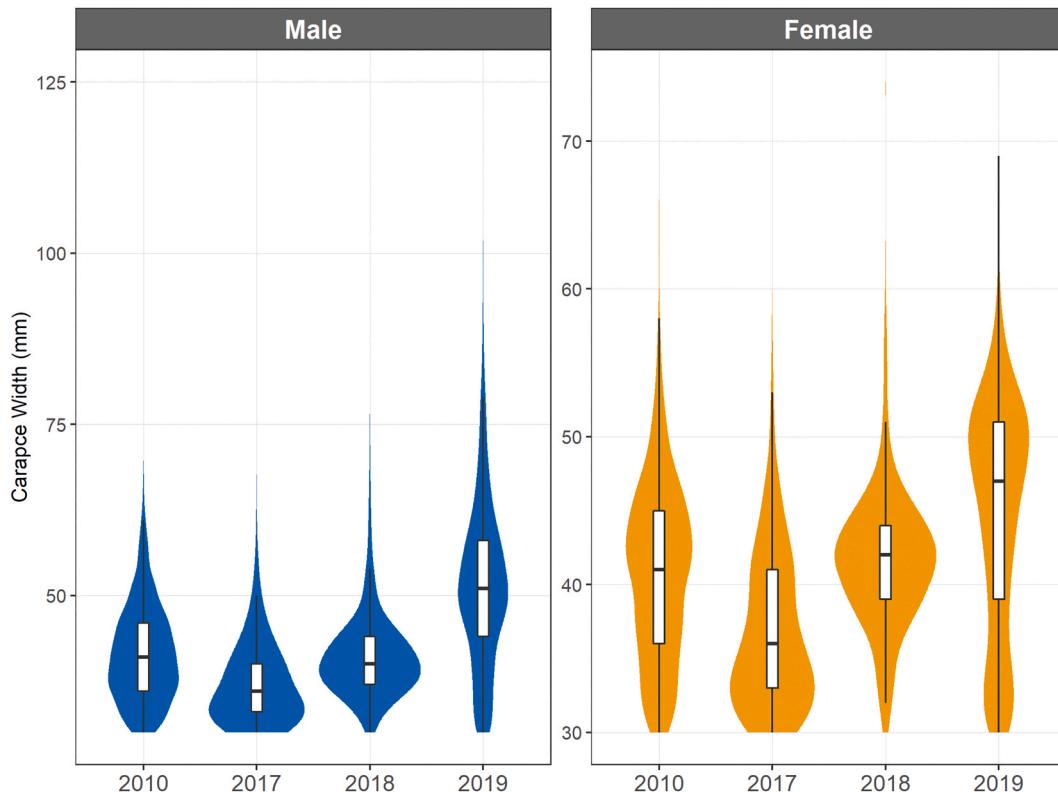


Fig. 4. Violin plot of northern Bering Sea male and female snow crab size distributions across years (2010, 2017–2019). Shaded areas represent the kernel probability density of size composition data. Box plots inside each violin plot summarize median population size (black bold horizontal line), and the 75th (upper horizontal line) and 25th (lower horizontal line) percentiles of the size distribution.

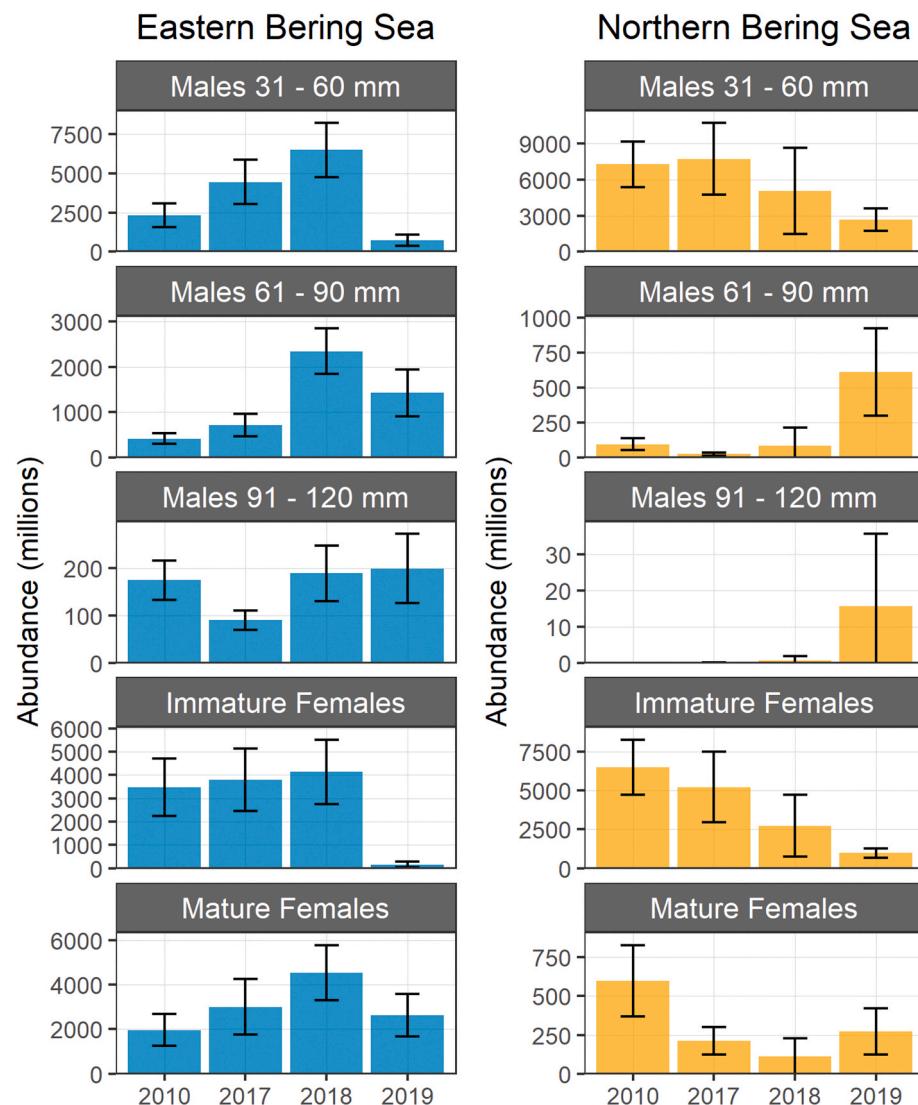


Fig. 5. Abundance ($\pm 95\%$ confidence intervals) of eastern Bering Sea and northern Bering Sea snow crab across years (2010, 2017–2019). Size and sex categories include males 31–60 mm carapace width (CW), males 61–90 mm CW, males 91–120 mm CW, immature females and mature females.

substantial size increase for both NBS males and females, in combination with a >2000% increase in the abundance of the largest size class of males from 2018 to 2019, resulted in a distinctly different size structure. Further, survey abundance estimates indicated substantial declines in small male and immature female snow crab across both EBS and NBS regions in 2019. These demographic shifts coincided with extreme warming in the Bering Sea, suggesting that potential temperature effects on recruitment, growth and survival may become increasingly important in shaping snow crab population structure under continued warming in the Bering Sea.

4.1. Thermal occupancy thresholds

The variability we observed in temperatures occupied by juvenile and adult snow crab confirms both ontogenetic changes in thermal preferences and differences in the strength of these temperature preferences across life history stages. Temperatures occupied by immature females and small males (31–60 mm CW) were well below 2°C prior to 2018, and persistently lower than that of older, larger snow crab. These findings are consistent with the cold (0 – 1.5°C), shallow-water habitats in which early benthic stages tend to settle and aggregate (Zheng et al., 2001; Dionne et al., 2003; Murphy et al., 2010). While temperatures of

occupancy were highly correlated with bottom temperatures across the 32-year study period, a 3-year decoupling of this trend in immature females and small males from 2015 to 2017 coincided with the start of the recent warm stanza in the EBS (Fig. 2). In 2014, average bottom temperatures in the EBS increased by nearly 1.5°C and abrupt shifts in immature female and small male spatial extent and centers of distribution preceded low temperatures of occupancy ($<0^{\circ}\text{C}$) from 2015 to 2017. These results suggest that the mechanism by which juvenile snow crab were able to maintain cold-water preferences during this 3-year warming period was through northward migration and range contraction in the EBS after settlement. However, telemetry studies have reported limited movement by juvenile snow crab (Cote et al., 2019), and observed shifts in spatial distribution of immature females and small males beginning in 2014 could instead indicate climate-driven changes in larval advection and the utilization of more northerly settlement and nursery grounds in the EBS. Understanding the relative importance of recruitment processes, settlement preferences and movement in determining patterns in thermal habitat use remains a challenge due to extensive ontogenetic migrations in snow crab.

Given the limited mobility of juvenile snow crab and potential inability to track temperature preferences, thermal occupancy is likely driven primarily by the availability of cold-water habitat in historic

settlement grounds east of St. Matthew Island, and juvenile snow crab may be especially vulnerable to continued warming in these nursery habitats. In 2018, for example, temperatures of occupancy converged at $\sim 3^{\circ}\text{C}$ across all size-sex categories. Consistent with observed reductions in the spatial extent of the EBS cold pool (Stabeno and Bell, 2019), thermal refugia $<2^{\circ}\text{C}$ were nearly absent in juvenile snow crab nursery grounds in 2018, and greatly reduced again in 2019. This finding suggests the potential for negative impacts on juvenile snow crab, which have historically avoided thermal habitats $>2^{\circ}\text{C}$ (Murphy, 2020). While occupancy temperatures for mature females and larger males also increased in response to warming from 2014 onwards, negative effects on metabolic processes are not apparent in mature snow crab until temperatures exceed 7°C (Foyle et al., 1989). Recent increases in EBS bottom temperatures, therefore, are likely still within the thermal threshold of larger individuals such that relocation may not be necessary. Relatively constant spatial distributions despite warming conditions might also suggest that factors such as predator or prey abundances may be more important in driving spatial distribution patterns than temperature. Nonetheless, as warming continues and thermal thresholds are reached, distribution shifts will be a necessary means to maximize exposure to suitable temperatures (Rutherford et al., 2015). Projected warming in the Bering Sea (Walsh et al., 2018) is expected to exacerbate the loss of suitable cold water habitat for juvenile snow crab, and in the absence of either relocation or acclimation, snow crab may be unable to tolerate warming temperatures.

4.2. Climate-mediated range contraction in the eastern Bering Sea

The hypothesis of density-dependent habitat selection predicts that as abundance declines, species will contract their range towards preferred habitats (Morris, 1987). In the EBS, groundfish species show a strong relationship between abundance and area occupied (Thorson et al., 2016). Likewise, Murphy et al. (2010) concluded that snow crab abundance explains more variation in area occupied than does bottom temperature. Our results, however, do not appear to support this finding. Density-dependent range contraction was not apparent even after accounting for variable responses across snow crab size and sex categories. We speculate that this disparity may be attributed to the additional 11 years of data in our study when compared to the analysis of Murphy et al. (2010). Our inclusion of data from 2009 to 2019 encompasses a greater range of temperature variability that may have revealed emerging climate effects on snow crab distribution. Directional shifts and range contraction in species distributions are often linked to temperature preferences (Kleisner et al., 2016), suggesting that a reduction in the spatial extent of snow crab is likely attributed to a loss of suitable thermal habitat. In warm years, snow crab may be unable to utilize warmer, deep habitats in the outer domain (100–170 m) and as such, cross-shelf migrations could be contracted to the middle domain as thermal preferences become increasingly more important than bathymetric cues.

Although modeling results indicated that latitudinal distribution shifts were not explained by climatic conditions, trends throughout the past decade still reflect thermal regimes in the EBS. A cold period from 2010 to 2014 coincided with a 5-yr southward shift in snow crab populations, which was then reversed in 2014 when warming began. Findings from a recent study indicated that snow crab centroids of abundance were best explained by the Arctic Oscillation and sea surface temperatures, and these linkages were attributed to relationships with recruitment (Szuwalski et al., in review). Snow crab recruitment is highly variable and episodic (Szuwalski, 2019), so large recruitment events may explain some of the deviance in spatial distribution indices as cohorts migrate from northern nursery grounds to warmer, deeper waters as they mature. While our study did not account for these potential cohort effects, inherent difficulties in disentangling the effects of climate and demographic structure on snow crab distribution shifts highlight the complexity in elucidating snow crab responses to warming

in the Bering Sea.

4.3. Cross-region declines in abundance of immature snow crab

Significant declines in the abundance of immature females and small males preceded by record-high temperatures of occupancy in 2018 could suggest both direct and indirect climate effects on snow crab survival. Although very few studies have examined direct temperature effects on late-benthic stages of snow crab, the stenothermic nature and narrow habitat requirements of juvenile snow crab indicate high vulnerability to warming temperatures (Dionne et al., 2003). High catches of immature females and small males at EBS survey stations $>3^{\circ}\text{C}$ in 2018 (Lang et al., 2018) followed by dramatic declines in 2019 at the same stations (Zacher et al., 2020) may suggest mortality rates that are sensitive to water temperatures and cold pool area. While these patterns could also be explained by juvenile redistribution to more favorable thermal habitats, widespread declines in abundance across both the EBS and NBS in 2019 suggest that migration was less likely. Overall, snow crab population declines observed in our study warrant future work to examine the effects of increasing temperatures on juvenile snow crab metabolic rates and thermal tolerance.

In addition to direct physiological effects, indirect mechanisms for mortality could include increased predation via climate-driven changes in the strength of spatial overlap between predators and prey (Hunsicker et al., 2013; Litzow and Ciannelli, 2008). Previous studies have shown that Pacific cod are a major predator of juvenile snow crab and as cod shift north, the relative importance of snow crab increases as a diet item (Livingston et al., 1993; Livingston and deReynier, 1996; Lang et al., 2003). Documented Pacific cod distribution shifts into the NBS and increases in cod biomass in important snow crab nursery areas south of St. Lawrence Island and Chirikov Basin (Stevenson and Lauth, 2019; Spies et al., 2019) may explain continued declines in immature snow crab abundance in the NBS since 2017. Although the scope of our study does not offer the means to explicitly test this hypothesis, the mean annual percentage of positive-catch snow crab stations in the NBS also occupied

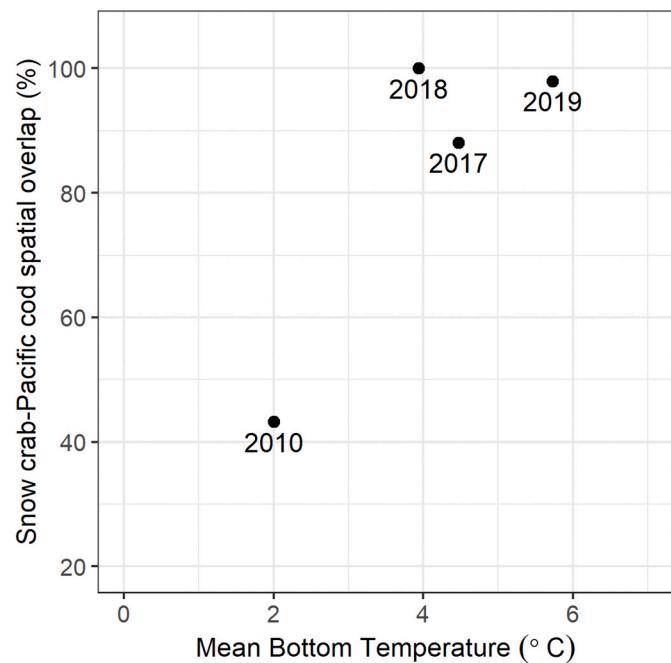


Fig. 6. The relationship between Pacific cod-snow crab spatial overlap (%) and average bottom temperatures in the northern Bering Sea. Annual spatial overlap metrics were estimated using the relative frequency of positive-catch snow crab stations also containing Pacific cod on NMFS NBS summer bottom trawl surveys (2010 and 2017–2019).

by Pacific cod increased from 43% to 88% from 2010 to 2017, and was nearly 100% in 2018 and 2019 (Fig. 6; Fedewa, unpublished data). These preliminary results may be indicative of a shift from bottom-up to top-down control as the structure and function of the NBS ecosystem change with the removal of thermal barriers to permit range expansion of novel predators such as Pacific cod into the NBS (Huntington et al., 2020). Pacific cod avoid waters less than 2°C (Giannelli and Bailey, 2005) and this cold water refugium was effectively absent for EBS snow crab in 2018, which may suggest increased cod–snow crab spatial overlap and predation in the EBS as well. The environmental ratchet hypothesis proposed that following an increase in bottom temperatures and northward contraction of the EBS snow crab stock in the 1980s, Pacific cod predation limited the re-colonization of southern areas during the return to a cold regime (Orensanz et al., 2004). However, our results are not consistent with this hypothesis as snow crab centers of distribution shifted south during the cold period from 2010 to 2014. Furthermore, the lack of evidence for a directional shift northward in our study during recent warming events could suggest an environmental ratchet in the sense that Pacific cod distribution shifts may, instead, truncate the northern extent of the snow crab geographical range and drive population centers southward owing to increased cod predation in more northerly latitudes. A re-evaluation of the environmental ratchet hypothesis following recent environmental and ecosystem changes in the Bering Sea may help to explain observed fluctuations in snow crab abundance observed in our study.

We cannot, however, eliminate the possibility that declines in abundance may be attributed to potentially confounding processes such as survey selectivity, catchability, or movement outside of the survey grid. Although the limited mobility of small snow crab would likely not support such large-scale distribution shifts outside of the surveyed area, the sampling efficiency of the 83–112 Eastern bottom trawl is size-dependent, and survey catchability is much lower for snow crab <40 mm CW (Somerton et al., 2013b). While we recognize these inherent constraints in deriving abundance estimates from survey data, continuing observations of reduced juvenile abundance in future years would provide support for the interpretation of mortality rather than catchability as the cause of the declines we document.

4.4. Shifts in size structure of northern Bering Sea snow crab

The 2019 increase in abundance of large snow crab in the NBS represents a dramatic contrast with previously-documented size distribution patterns (Chilton et al., 2011; Kolts et al., 2015; Lang et al., 2018). However, the origin of these large individuals in the NBS remains unclear. Trends in snow crab centers of distribution provided little support for migration into the NBS following recent warming in the EBS, although given the large geographic range of snow crab, it is possible that population-level spatial indices developed for this study do not effectively capture shifts northward in smaller portions of the population. Results of the 2019 EBS bottom trawl survey indicate an aggregation of legal-sized male snow crab in close proximity to the northern extent of the EBS survey grid, while most large snow crab caught in the NBS were concentrated in the southwestern corner of the NBS survey grid (Zacher et al., 2020, Fig. 106). These observed spatial distribution patterns suggest a contiguous distribution of snow crab between the two regions, providing support for the hypothesis of migration into the NBS and emphasizing the continued need to survey both regions in the Bering Sea. Furthermore, tagging studies on mature male snow crab in the EBS have documented migrations of over 100 km in one direction (Nichol and Somerton, 2015) and 250 km migrations over a 10-month period (Nichol et al., 2017), indicating that large snow crab are highly mobile and capable of large-scale distribution shifts. Latitudinal distribution shifts may not, however, be an immediate response to 2018–2019 warming events in the Bering Sea. Previously documented northward range contractions by EBS snow crab were lagged up to 6 years following a warm period (Orensanz et al., 2004), which suggests that snow crab

may only respond to environmental changes after conditions prevail for several years. If responses are in fact lagged, we would expect to detect large male snow crab in the NBS first, given their high mobility and broad range in the EBS.

Direct temperature effects on molt frequency, growth rates and size at maturity may also explain recent shifts in the size structure of NBS snow crab. Prior to warming in 2014–2019, the NBS was characterized by very cold summer bottom temperatures (<0 °C). These temperatures drive decreased molting probabilities and smaller growth increments in immature snow crab, which in turn are thought to explain declines in mean carapace width and size at maturity with increasing latitude (Otto, 1998; Orensanz et al., 2007; Burmeister and Sainte Marie, 2010). Temperature-specific logistic models for female snow crab in the Canadian Atlantic show that temperature increases from -1 °C to 4 °C result in a nearly 15 mm CW increase in the size at which 50% of the population is mature (Dawe et al., 2012). Results from that study also showed the highest incidence of skip molting at -1 to 0 °C, with molting frequency increasing at higher temperatures. Average temperatures in the NBS exceeded 4 °C in 2017 and reached nearly 6 °C in 2019 (Fig. 2), suggesting that warming may be responsible for increased growth potential and molt frequency that would explain the presence of large individuals in the NBS. Previous attempts to detect the modal progression of snow crab cohorts across years in the NBS have been complicated by irregular molting and slow growth (Kolts et al., 2015). Increasing size distributions during 2017–2019 are consistent with cohort growth, as evidenced by the rate of change in median sizes for males and females (Fig. 4). Although growth-per-molt equations have only been developed for the EBS snow crab stock (Somerton et al., 2013a) and temperature-dependent growth rates have yet to be determined, warmer temperatures in the NBS could drive an annual molt and larger growth increments in NBS snow crab. It is therefore possible that male and female cohorts within our NBS study area in 2017 grew to the sizes documented in 2019 (~15–30 mm increase in median CW). On the other hand, such large increases in growth increments may be unattainable for NBS snow crab in a 3-year period given that changes in growth and size at maturity in snow crab appear to be conditioned by temperatures throughout the life history and likely operate at much longer time scales (Dawe et al., 2012). Size structure of snow crab in the Chukchi Sea has been explained by a suite of environmental factors (Konar et al., 2014), and the presence of commercial-size male snow crab in the cold, offshore waters of the Beaufort Sea (Legerwell et al., 2011; Divine et al., 2019) suggests that mechanisms other than temperature such as benthic prey quantity or quality may contribute to shifts in NBS size structure. Furthermore, given the cyclical nature of snow crab recruitment and challenges in tracking pseudocohorts, interannual shifts in size composition are expected, and disentangling the relative importance of immigration, temperature-dependent growth, and cohort effects on NBS snow crab demographic structure remains challenging with limited data available for the NBS.

5. Conclusions

Overall, our study demonstrates that shifts in the spatial extent of snow crab are driven by climatic conditions in the EBS and thermal occupancy patterns depend on the availability of cold water habitat. Continued warming in the Bering Sea could necessitate range contraction northward to more suitable thermal habitat, while top-down effects of Pacific cod predation may prove to be increasingly important in shaping spatial distribution and demographic structure of juvenile snow crab. Our results revealed a substantial increase in large male and mature female snow crab in the NBS coincident with increases in water temperatures, although it is unclear whether movement between the EBS-NBS border or increased growth potential contributed to the documented shift in size structure. While these results could be indicative of a self-sustaining mature snow crab population and future fishery in the NBS, the cascading effects of continued warming, increased

predation and declines in juvenile snow crab suggest the potential for opposing, negative effects on snow crab production in years to come. As the NBS continues to warm, a boundary between the two regions will likely lack biological meaning for snow crab and necessitate management considerations. The current EBS snow crab stock assessment is not spatially explicit and fits to survey biomass and size composition data only account for crab caught within the EBS survey area (Szuwalski, 2019). However, management boundaries for the fishery do extend into the NBS. Our finding that large, legal-size males exist outside of the EBS survey grid highlights the need to incorporate NBS survey data in deriving mature male biomass estimates and biological reference points. Further, spatial mismatch between large male abundance during the summer survey and the distribution of catch during the winter fishery suggests the need to characterize seasonal movement across the EBS-NBS border. An important caveat to our study is that results are only applicable to a small temporal window during the summer bottom trawl survey and may not be representative of patterns in winter months during the directed fishery. Future tagging studies may help to clarify the origin of large snow crab captured during summer surveys in the NBS, and determine if large males migrate southward to fishing grounds in the winter, thus warranting the inclusion of NBS survey data in the stock assessment. Overall, the challenge in managing a spatially-structured stock prone to climate-driven distribution shifts emphasizes the importance of developing spatially structured assessment methods (Szuwalski and Punt, 2015), and targeted research to understand snow crab recruitment vulnerabilities and responses to continued warming (Stortini et al., 2015).

Author statement

Erin Fedewa: Conceptualization, Methodology, Writing- Original draft preparation, Validation. **Tyler Jackson:** Software, Methodology, Writing- Reviewing and Editing. **Jon Richar:** Data Curation, Visualization, Software. **Jennifer Gardner:** Writing- Reviewing and Editing. **Michael Litzow:** Conceptualization, Methodology, Writing- Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr2.2020.104878>.

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