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New estimates of weight-at-size, maturity-at-size, fecundity, and biomass of snow crab, *Chionoecetes opilio*, in the Arctic Ocean off Alaska

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Abstract

Snow crab (*Chionoecetes opilio*) were identified as a potential future target fishery species in federal waters of the Arctic Ocean off Alaska by the Arctic Fishery Management Plan (Arctic FMP) in 2009, but this plan currently prohibits commercial harvest until sufficient information is available to assess a sustainable commercial fishery. One drawback of the current Arctic FMP is that critical population and biomass estimates were based on limited data. Collaborative research efforts in the Chukchi and Beaufort seas over the past decade have yielded a much richer database on snow crab in the Arctic. Using these data, we generated new estimates of weight-at-size, maturity-at-size, fecundity, and biomass to recalculate sustainable yield of snow crab in the U.S. Arctic. Weight-at-size was generally similar for male and female snow crab between the Chukchi and Beaufort seas, with males reaching overall larger sizes than females in both seas and largest male crabs occurring in the Beaufort Sea. Compared with snow crab in other geographic regions, 50% morphometric maturity was reached at a slightly smaller size in the Chukchi Sea; low sample sizes in the Beaufort Sea prevented maturity-at-size analysis. Fecundity-at-size in the Chukchi Sea was similar to known values estimated for snow crab in other regions. Estimated total reproductive output, using fecundity estimates obtained here, suggest that local reproduction may be sufficient to account for a large portion of observed small juvenile benthic snow crab abundances; further investigation is warranted to determine whether Chukchi and Beaufort populations are self-sustaining at this time. Although snow crab had high abundances in the Chukchi Sea, harvestable biomass of male snow crab only occurred in the Beaufort Sea because crab larger than the minimum marketable size (≥ 100 mm carapace width, based on Bering Sea metric) were absent in the Chukchi Sea over the study period. Our biomass estimates in the Chukchi Sea were substantially higher than previous estimates, owing at least in part to high abundances of small crab that were greatly under-sampled with the large-mesh gear such as was used in surveys referenced in the Arctic FMP. Estimates of biomass and sustainable yield for the Beaufort Sea were over twice as high as previous estimates in the Arctic FMP, but harvestable biomass was largely limited to the slope (> 200 m depth) and is unlikely to support commercial harvest. Our results expand overall understanding of arctic snow crab dynamics in light of potential future fisheries or other, non-fishing activities and inform the management of the Alaskan Arctic stock.

Key words: Arctic Fishery Management Plan (Arctic FMP); Beaufort Sea; Chukchi Sea; female reproductive potential; maturity; sustainable yield

1. Introduction

Snow crab *Chionoecetes opilio* are distributed across subarctic and Arctic waters, with lucrative commercial fisheries occurring in the North Atlantic (eastern Canada and Greenland), Bering Sea, and Sea of Japan. The eastern Bering Sea (EBS) fishery is one of the most valuable fisheries in the US, with an average harvest of 25,700 metric tons (56.6 million pounds) and an average ex-vessel value of $133 million dollars in 2017 (ADF&G 2018, Fissel et al. 2018). Harvest is limited to only males at or above a marketable size (≥ 100 mm carapace width [CW]) in an attempt to protect the reproductive potential of mature females (Sainte-Marie and Gilbert 1998, Zheng and Kruse 2006, Turnock and Rugolo 2012). In 1999, the EBS snow crab fishery was declared overfished after a period of declining snow crab biomass and abundance (Turnock and Rugolo 2012). Additionally, a northward contraction of the center of snow crab distribution in the EBS in response to changing oceanographic conditions was identified shortly after overfishing was recognized (Zheng et al. 2001, Orensanz et al. 2004). The combination of the biomass decline, distributional shift, and high abundances of snow crab north of the Bering Strait (NPFMC 2009, Kolts et al. 2015) raised fisheries concerns about the possibility of this species moving out of the primary EBS fishing grounds and northward into Arctic waters (Mueter et al. 2012, Hollowed et al. 2013). In response to a potential future snow crab fishery in the Alaskan Arctic, the Arctic Fishery Management Plan (Arctic FMP) was developed in 2009 by the North Pacific Fishery Management Council (NPFMC 2009). The Arctic FMP relied on limited available data (from 96 sampling stations in the Chukchi Sea and 26 sampling stations in the Beaufort Sea) and borrowed life history metrics from other regions to evaluate total and harvestable biomass of snow crab in the Chukchi and Beaufort seas.

The Arctic FMP currently presumes exploitable snow crab biomass to be low in the Alaskan Arctic, although snow crab are dominant members of benthic communities with respect to biomass and abundance in the Chukchi Sea, and occur at commercial sizes (≥ 100 mm CW based on the standard for the EBS) in the western Beaufort Sea (Bluhm et al. 2009, Rand and Logerwell 2011, Ravelo et al. 2014, 2015). In the Chukchi Sea, snow crab contribute significantly to overall invertebrate biomass, even at small maximum sizes (i.e., 74 mm CW, Frost and Lowry 1983, Paul et al. 1997, Rand and Logerwell 2011, Konar et al. 2014, Ravelo et al. 2014, Gross et al. 2017). The potential commercial exploitation of snow crab in the Arctic requires detailed, region-specific knowledge of stock structure and life history. However, snow crab in the Chukchi and Beaufort seas have not been historically monitored with any regularity due to the lack of dedicated federal monitoring programs and challenges of sampling the vast, seasonally ice-covered shelves and slopes of these regions. Limited available data (i.e., Frost and Lowry 1983, Paul et al. 1997) suggest that snow crab abundance has increased on the Chukchi shelf by at least an order of magnitude over the last few decades, although snow crab sizes remain small (maximum size: 74 mm CW, Gross et al. 2017). Abundance in the Beaufort Sea has also increased (Paul et al. 1997, Logerwell and Rand 2010), and the reported maximum size of snow crab in the Beaufort Sea has increased from 75 mm CW in the 1970s (Frost and Lowry 1983) to 119 mm CW in the 2000s (Rand and Logerwell 2011), although expanded study areas within in this region may account for observation of larger snow crabs.

A clear understanding of growth and maturation processes, population structure, and fecundity is essential for effective management of snow crab fisheries (Comeau and Conan 1992, Sainte-Marie et al. 1995), including the development of sustainable harvest limits (NPFMC 2009). Snow crab growth and allometry has been best-studied in geographic regions where snow crab comprise an important commercial fishery resource (e.g., Gulf of St. Lawrence: Watson 1970, Haynes et al. 1976, Sainte-Marie et al. 1995; Newfoundland: Comeau and Conan 1992, Comeau et al. 1998; EBS: Haynes et al. 1976, Otto 1998, Orensanz et al. 2007, Ernst et al. 2012). Population data from the North Atlantic, chiefly the Gulf of St. Lawrence, are currently applied to growth estimates of snow crab in less-studied arctic regions, such as the northern Bering, Chukchi, and Beaufort seas (Kolts et al. 2013, Gross et al. 2017). Snow crab undergo a series of molts during which they exhibit discrete increases in body size (Hartnoll 1982). Individuals undergo a final, terminal molt to maturity between instars X-XIII (≥ ~54 mm CW based on crab in Canadian Atlantic), but size at terminal molt is highly variable among individuals (Conan and Comeau 1986, Comeau and Conan 1992, Comeau et al. 1998, Sainte-Marie et al. 1995, 2008, Burmeister and Sainte-Marie 2010). Somatic growth for males and females is similar at small sizes (i.e., benthic instars I-VII, Comeau et al. 1998), but male molt increments are larger at later stages, with terminal molt occurring earlier in females, resulting in larger maximum sizes for males relative to females (Alunno-Bruscia and Sainte-Marie 1998). Growth models have established mean size-at-instar for each stage, e.g., in the northern Atlantic (Sainte-Marie et al. 1995) and the EBS (Orensanz et al. 2007, Ernst et al. 2012). These growth models have been widely applied to other stocks across the geographic range of snow crab (e.g., northern Bering Sea: Kolts et al. 2013, Chukchi Sea: Gross et al. 2017). In cold waters (< 0°C) snow crab may have smaller growth increments per molt, longer intermolt periods, or skip a molt (Orensanz et al., 2007, Burmeister and Sainte-Marie 2010), all of which can contribute to slow growth and complicate application of growth models from subarctic to Arctic populations.

Maturity-at-size is a critical determinant of reproductive output and rate of population growth in brachyuran crabs (Stearns 1976, Hines 1982). Male snow crab exhibit an allometric increase in chela height (CH) relative to body size (CW) during the terminal molt (Conan and Comeau 1986) and this relationship is used to determine maturity status for males. However, gonad development occurs prior to terminal molt and males may be sexually mature prior to exhibiting the change in chela allometry (Sainte-Marie et al. 1995). Females experience a marked increase in the size of their abdominal flap to accommodate an egg clutch after their terminal (maturity) molt (Watson 1970, Moriyasu et al. 1987, Alunno-Bruscia and Sainte-Marie 1998). In a latitudinal gradient from the southeastern Bering Sea to the Chukchi Sea, size at 50% maturity in female snow crab decreases, possibly due to a decrease in temperature (Armstrong et al. 2008, 2010, Kolts 2012). This latitudinal pattern of smaller individuals occurring at higher latitudes has also been established for both males and females in the Gulf of St. Lawrence (Sainte-Marie and Gilbert 1998, Dawe et al. 2012), Greenland (Burmeister and Sainte-Marie 2010), and Newfoundland (Dawe et al. 2012).

Female fecundity (average number of eggs in a clutch) and lifetime female fecundity (cumulative number of eggs produced in a lifetime), and their contributions to population-level reproductive output, are important metrics regarding stock productivity and also in understanding distribution patterns and changes in crab stocks (Armstrong et al. 2008). Female fecundity of brachyuran crabs is a function of body size, with larger females producing larger egg clutches (Orensanz et al. 2007, Kolts et al. 2015). In the eastern and northern Bering Sea, mean annual cold bottom temperatures ($\leq$ ~1 °C) result in a shift from an annual to a biennial breeding cycle for female snow crab (Moriyasu and Lanteigne 1998, Rugolo et al. 2005, Webb et al. 2007, Sainte-Marie et al. 2008, Kolts et al. 2015). For snow crab in the U.S. Arctic off Alaska, it is likely that at least a portion of female snow crab also experience biennial brooding given that bottom temperatures $\leq$ 1 °C are regularly recorded across the shelves (Grebmeier et al. 2015, Danielson et al. 2017). It is unknown if mature biomass is sufficient to sustain local populations in the Chukchi and Beaufort seas, regardless of whether annual or biennial brooding cycles dominate, or if advected larvae from southern regions at least partially support, or merely add to, local production (Bluhm et al. 2015). No mature females with fertilized egg clutches have been collected in the Beaufort Sea to date (Bluhm et al. 2015), indicating no evidence of local reproduction in this region.

The goal of the present study was to provide new information on snow crab life history and distribution trends in the Chukchi and Beaufort seas, using a synthesis of available data collected over 2004-2017. Specifically, we estimated (1) individual weight-at-size for snow crab in the Chukchi and Beaufort seas, (2) maturity-at-size and fecundity-at-size for snow crab in the Chukchi Sea only, due to low sample sizes in the Beaufort Sea, (3) potential reproductive capacity of mature females in the Chukchi Sea only, and (4) regional biomass, abundance, and sustainable yield for snow crab in the Chukchi and Beaufort seas. Our estimates of weight-at-size, maturity-at-size, and fecundity improve previous biomass assessments by applying region-specific population metrics as much as possible. We then used these direct parameter estimates to revise total and harvestable biomass estimates originally published for snow crab in the Arctic FMP (NPFMC 2009).

2. Methods

2.1 Snow crab collections

This project used a combination of snow crab data collected from a total of 20 surveys, 13 in the Chukchi Sea and 7 in the Beaufort Sea, between 2004 and 2017 (Table 1, Fig. 1). Samples and data were used in various combinations to address project objectives (Table 1), depending on availability. A vast majority of crab for this study were collected with a plumb staff beam trawl (PSBT, modified from Gunderson and Ellis 1986, see details on towing methods in Norcross et al. 2015, Table 1). The PSBT had a 2.257 m opening and a net mesh of 7 mm with a 4 mm cod end liner. Tow duration lasted from 1 to 6 min at speeds ranging from 0.5 to 0.75 m s^{-1}. Crab were also collected using an 83-112 eastern bottom trawl (EBT, Table 1). The EBT is the standard net for the National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC) bottom trawl surveys in the EBS. The EBT had a 25.3 m headrope and 34.1 m footrope. During the Arctic Eis 2012 survey (Table 1), the EBT was fitted with a net mesh of 10.2 cm, with 8.9 cm intermediate and codend liners. The codend also had a 3.2 cm liner (Goddard et al. 2012). Tow duration for the EBT ranged from 5 to 15 min at an approximate speed of 1.5 m s^{-1}. Snow crab collected from all trawls were rinsed, sexed and counted, bulk weight per station was recorded using spring or digital hanging scales, and in some instances individual CW (standard measure of body size) was measured to the nearest 0.1 mm using digital Vernier calipers. Select crab were either frozen whole or preserved in formalin (RUSALCA 2009 only) for transport to the laboratory. Crab were then thawed (if frozen), blotted dry, and individually weighed to the nearest 0.1 g. For all males, chela height (CH; standard measure of maturity) was measured for the left chela to the nearest 0.1 mm using digital Vernier calipers consistent with Conan and Comeau (1986). Occasionally, crab experienced limb loss during collections or after freezing, or were collected with missing limbs. If limbs could be preserved with the whole crab they were. A small number of crabs had missing limbs that were not able to be recovered. In these cases, the weight for each missing limb was estimated from the matching limb on the other side of the same crab or the corresponding leg of a crab of a similar size and applied to the total weight to account for missing limbs.

2.2 Weight-at-size

As a proxy of individual weight-at-size of crab, we used the allometric relationship between weight (individual biomass, g) and size (mm CW) of measured crab. Individual wet weight (g) and size (mm CW) for males and females collected in the Chukchi and Beaufort seas were log-transformed and weight-at-size was estimated from a linear regression as:

$$\log(\text{Weight}(g)) = a + b*\log(\text{CW}(mm)),$$

where log is the natural logarithm, *a* is the intercept and *b* is the slope. Analyses of covariance (ANCOVA) with separate slopes by region were performed to determine if weight-at-size differed significantly between the Chukchi and Beaufort seas for males, immature females, and mature females, respectively. Females were separated into immature and mature status because mature females have terminally molted and allocate energy to reproductive tissue growth and production (i.e., gonad and egg clutches) rather than somatic growth (Alunno-Bruscia and Sainte-Marie 1998).

Size frequency distributions (SFD) for all size data available, pooled across years, were examined separately for the Chukchi and Beaufort seas to characterize the size ranges of male and female crab in each region. We were unable to fit mixture models to objectively distinguish modes in the SFD for snow crab in either region and, therefore, did not attempt to interpret modal peaks observed in SFD histograms as instars.

2.3 Mean individual crab weight across survey area

To examine spatial variability in the size of snow crab across the Chukchi and Beaufort shelves, mean weight by haul was modeled separately within each sea using a thin-plate regression spline smoother within a Generalized Additive Modeling (GAM) framework. Mean individual weight in each haul containing crab was first computed by dividing the total weight of snow crab in a given haul (measured in the field as bulk weight, kg) by the number of snow crab caught. Individual weights were then fourth-root transformed to normalize residuals and were modeled as:

$$W_{ti} = \alpha + s(x_{ti}, y_{ti}) + \varepsilon_{ti},$$

where W_{ti} is the fourth-root transformed mean weight at station *i* during year *t*, α is the overall intercept, s denotes a smooth function of sampling location described by distances x and y (in km) from an arbitrary origin, and ε_{ti} are residuals that are assumed to be normally distributed with a zero mean and variance σ^2. The estimated mean sizes were then mapped over the study regions. We also considered a mixed effects model with a random-year effect to account for differences in mean size by year. However, the random-year effect did not result in a better model fit based on the Akaike Information Criterion and years were, therefore, pooled in the analysis.

2.4 Maturity-at-size

Maturity-at-size for male crab was determined as the proportion of males exhibiting morphometric allometry in the left chela at a given body size (Conan and Comeau 1986). This was only possible for Chukchi Sea crab as sample sizes were too low in the Beaufort Sea. To assign a breakpoint for male maturity, observed male CW and left CH were plotted against several published regression relationships (i.e., from the EBS, Kolts et al. 2013; and eastern Canadian Atlantic, Comeau et al. 1998). The EBS data presented the best fit for allometric male snow crab data in the Chukchi Sea; thus, mature males were distinguished from juvenile and adolescent males by using the established dividing line of CH = 0.191 x CW (Kolts et al. 2013). Female maturity-at-size in the Chukchi Sea only was estimated as the proportion of females exhibiting a change in allometry in the abdomen relative to body size (i.e., large flap covers the entire ventral side of mature females, Paul et al. 1997) or presence of an egg clutch (Jewett 1981). The proportion of mature female crab at a given size was estimated by fitting a logistic regression model with a logit link to binary maturity data (mature= 1, immature= 0) as a function of size:

$$\log(p_k/(1-p_k)) = \alpha + \beta * CW_k(\mathrm{mm}),$$

where p_k is the proportion of mature females in size class *k*, α and β are linear regression parameters on the logit scale, and the model was fit by maximizing the binomial likelihood. Size at 50% maturity was then estimated as $-\alpha/\beta$, corresponding to the size at the inflection point of the logistic curve.

To correct for gear bias in the size composition estimate of the individuals used to determine size-at-maturity in the Chukchi Sea, we compared the size frequencies of crab between the PSBT and EBT based on snow crab CW data from 33 paired trawls taken during the Arctic Eis 2012 cruise (Britt et al. 2013, Table 1). The paired trawl samples were distributed throughout the study area and are representative of the full latitudinal and depth range of the survey (Kotwicki et al. 2017). The observed size composition was summarized by gear type as the number of crab per km^2 in each 1 mm size bin. The effectiveness of the two nets for sampling snow crab in their path (catchability) is unknown and is likely to differ among crab sizes (size selectivity). Assuming each trawl is fully size selective (selectivity = 1) over some range of observed sizes (CW), the size selectivity of the two trawl types can be estimated under the following assumptions. We first used the common assumption that selectivity follows a logistic model of the form:

$$\text{selectivity} = \frac{1}{1+e^{b(x-a)}},$$

where *x* is the carapace width (mm CW), parameter *a* corresponds to size at 50% selectivity, and *b* corresponds to the steepness of the curve. We further assumed that selectivity of the EBT approaches 1 for large crab (large mesh size) and selectivity may decrease with decreasing CW

($b > 0$), whereas the PSBT has full selectivity for small snow crab (small mesh size) and selectivity may decrease with increasing CW ($b < 0$).

We simultaneously estimated the parameters of the two selectivity curves by minimizing a weighted sum of squared differences between the predicted number of crab at size k from the PSBT and the predicted number of crab at size k from the EBT. Because the variability in numbers at size was not constant and increased with the number of crab (N_k) in size bin k, we applied appropriate weights to the squared differences before summing across size bins. We assumed that variance increases linearly with N_k based on the expected mean-variance relationship for Poisson-distributed count data. We then weighted the squared difference for each size bin by $1/N_k$, where N_k values were computed from a smoothed length-frequency distribution that was estimated by minimizing the unweighted sum of squares. If the number of crab in a given size bin was estimated to be less than 1 it was set equal to 1 to avoid assigning excessive weights to these bins. This selectivity analysis was used to determine a size range over which both gears had similar high selectivity to pool snow crab abundances and biomass across gear types. Estimated size selectivity was used to estimate the "true" size distribution of crabs in the Chukchi Sea by dividing the observed numbers at a given size by the estimated selectivity at that size. The methods used in the present study differ from previous biomass estimates in the Arctic FMP in that the Arctic FMP used only data collected with the EBT that were not corrected for selectivity (NPFMC 2009).

2.5 Fecundity and egg production

Mean fecundity at size was estimated using the number and weight of eggs taken from 322 mature females collected during the RUSALCA 2009 and 2012, COMIDA 2010, CSESP 2010 and Arctic EIS 2012 cruises in the Chukchi Sea (Table 1). Each total egg clutch was removed from the pleopods, 250 eggs were subsampled and dried at 60 °C to a constant weight, and the dry weight of the subsample was determined (Stichert 2009, Webb et al. 2016). The remaining egg mass was also dried as described above to obtain total dry weight. Individual fecundity was then estimated by dividing the weight of the total egg mass by the average dry weight of the eggs in the sub-sample and multiplying by the number of eggs in the sub-sample (n= 250). Finally, a linear regression of the logarithm of total number of eggs (dependent variable) on log-transformed carapace width (CW, independent variable) for each crab was used to determine the relationship between body size and mean number of eggs in a clutch.

To estimate total egg production in the Chukchi Sea, we first estimated the abundance of mature females in the Chukchi Sea in 2012 based on the observed density of females at each station (number of females per km^2) and the estimated maturity-at-size relationship. Only data from the 2012 gridded Arctic Eis survey, which had the most complete spatial coverage, were used for this estimate to avoid biases associated with temporal or spatial differences in distribution and fecundity. Station-specific densities of mature females for each 1 mm CW increment were first estimated as the proportion of mature females from the logistic maturity-at-size curve multiplied by the total density of females in a given size class (CW) at a station. The total abundance of mature females in the survey area by CW was then estimated by multiplying station-specific densities by the area of the grid cell represented by each station and summing abundances across all grid cells. For each size class (1 mm CW increments), we then multiplied the average fecundity at size (number of eggs per mature female) by the number of mature females in a given size class and summed the number of eggs across size classes for an estimate of total annual egg production.

2.6 Biomass, abundance, and sustainable yield

Biomass and abundance per unit effort at each station were estimated based on the weight and number of crab caught at each station and the area swept by the trawl. For the EBT, area swept was determined by multiplying the distance towed by the mean net spread. For the PSBT, the net width was assumed to be fixed at 2.257 m (Gunderson and Ellis 1986), and area swept was equal to the net width multiplied by the distance towed as calculated during each tow. Catches were standardized by computing catch per unit effort (CPUE) for each haul in biomass (kg) or numbers per km^2. Crab densities (CPUE) were then estimated using a thin-plate regression spline smoother within a GAM framework (Wood 2017). Sampling locations differed among years and cruises, but substantial overlap among cruises allowed us to estimate inter-annual differences in mean CPUE, assuming that the spatial patterns in CPUE were consistent over time. Therefore, we modeled CPUE as a function of year and location as follows:

$$\mathrm{CPUE}_{ti} = \alpha + a_t + s(x_{ti}, y_{ti}),$$

where CPUE_{ti} is the observed density at station *i* during year *t*, α is the overall intercept, a_t is a random intercept associated with year *t* to account for interannual differences in mean CPUE, and s denotes a smooth function of sampling location. To preserve distances in the east-west (x) and north-south (y) directions, locations were calculated as the great-circle distance, projected onto a plane, from an arbitrarily chosen origin in the southwest corner of the study area. Preliminary analyses suggested that biomass values were strongly right-skewed, included a number of zeros, and that the variance tended to increase with mean density. These features could best be modeled using a Tweedie distribution (Dunn and Smyth 2005), where variance is given by the mean to the power *p*, and *p* is estimated but constrained to range from 1 (corresponding to a Poisson distribution) to 2 (gamma distribution). Models were fit separately to the Chukchi and Beaufort seas data and densities were predicted for the center of each grid cell in a 10 x 10 km grid overlaid on the survey area. Total biomass within each area was then estimated by multiplying the predicted mean density in each grid cell by 100 to obtain an estimate of total biomass within the 100 km^2 grid cell, then summing over all grid cells. Uncertainty in total biomass was estimated by repeatedly simulating predicted values for each grid cell from the posterior distribution of the smoothing parameter estimates and computing total biomass as described above. Estimates were obtained over the total survey area in the U.S. Chukchi Sea (172,000 km^2), and the total survey area in the U.S. Beaufort Sea (64,400 km^2). In addition, we obtained separate estimates for the U.S. Chukchi Sea south and north of Point Hope, Alaska, to account for potential differences between the southern and northern Chukchi Sea. Estimates obtained here were considered pristine, or unfished, biomass for comparison with previous estimates from the Arctic FMP (NPFMC 2009). For comparison, we determined the equilibrium biomass at a given fishing mortality following the approach in the FMP, updated with new estimates for weight-at-size and maturity-at-size:

$$\mathrm{B(F|r)} = \left[\left(\frac{h}{M+F}\right)\left(1+\frac{1}{(M+F)d}\right)\right]^{\frac{1}{r}},$$

where *h* is the scale parameter in Cushing's (1971) stock-recruitment relationship, *M* is the instantaneous natural mortality rate, *F* is the instantaneous fishing mortality, *d* is the difference between the age-at-maturity and the age intercept of the linear weight-at-age equation, and *r* is the amount of resilience implied by the stock recruitment relationship (NPFMC 2009). We used the default value of *M* for the Bering Sea snow crab stock (M=0.23; Turnock and Rugolo 2008) and obtained our own parameter estimate for *d* from this study, which resulted from direct estimates of weight-at-size and maturity-at-size (see above sections), combined with previous literature for weight-at-age of snow crabs in the Chukchi Sea (Gross et al. 2017), and assuming a intercept of zero for the linear weight-at age-equation (NPFMC 2009). To determine the amount of biomass available to future potential fisheries given the new biomass estimates, we determined sustainable yield (Y) as the product of F and equilibrium biomass:

$$\mathrm{Y}(F|r) = F \cdot B(F|r).$$

We then obtained an estimate of the instantaneous fishing mortality that maximizes equilibrium yield as:

$$\mathrm{F}_{\mathrm{MSY}}(\mathrm{r}) = \left(\frac{M}{2(1-r)}\right)\left(1 - \frac{2-r}{M*d} + \sqrt{\left(\frac{(2-r)}{M*d}\right)^2 + \frac{4-6r}{M*d} + 1}\right) - M.$$

The biomass at which a maximum sustainable yield (MSY) can be obtained was calculated as:

$$\mathrm{B}_{\mathrm{MSY}} = \mathrm{B}\mathit{ratio}(\mathrm{F}_{\mathrm{MSY}}(\mathrm{r})|\mathrm{r}) \cdot \mathrm{B}_0,$$

where B*ratio* is the ratio of equilibrium biomass to unfished (pristine) biomass (B_0). Finally, MSY was estimated as:

$$\mathrm{MSY} = \mathrm{Y}\mathit{ratio}(\mathrm{F}_{\mathrm{MSY}}(\mathrm{r})|\mathrm{r}) \cdot \mathrm{B}_0,$$

where Y*ratio* is the ratio of sustainable yield to B_0. We compared our estimates of biomass and sustainable yield to values in the Arctic FMP (NPFMC 2009).

3. Results

3.1 Size-frequency-distributions and weight-at-size

Although males were much less abundant in the Beaufort Sea than in the Chukchi Sea (Fig. 2A-C), the largest Chukchi male (86 mm CW, Fig 2B) was approximately 33 mm smaller than the largest male collected in the Beaufort Sea (119 mm CW, Fig. 2C). The largest female snow crab in the Chukchi Sea were also smaller than males (66 mm CW, Fig. 3A), and they reached larger maximum sizes in the Beaufort Sea than females in the Chukchi Sea (83 mm CW, Fig. 3B). Immature females in the Chukchi Sea ranged from 4 to 58 mm CW and mature females ranged from 21 to 66 mm CW (overlapping by 37 mm CW, Fig. 3). In the Beaufort Sea, immature females ranged from 16 to 70 mm CW and mature females ranged from 37 to 82 mm

CW (overlapping by 33 mm CW; Fig. 3). We collected high numbers of early benthic instars (i.e., 3-20 mm CW) in the Chukchi Sea (Fig. 2A and 3A); few small, presumably juvenile, crab were collected in the Beaufort Sea (Fig. 2C and 3B).

From 2004 to 2017, approximately 3,416 snow crab were individually measured and weighed across the Chukchi and Beaufort seas. Weight-at-size was similar for males between the Chukchi and Beaufort seas (ANCOVA, $p= 0.72$, Fig. 4A-B) as well as for pooled immature and mature females between the Chukchi and Beaufort seas (ANCOVA, $p= 0.63$, Fig. 4C-D). However, females in the Chukchi Sea reached heavier weights than Beaufort Sea females at larger sizes (ANCOVA, $p< 0.0001$ for both immature and mature females). When considering immature versus mature female weight-at-size within each region, we found contrasting patterns. Mature females in the Chukchi Sea achieved heavier weights at a given size than immature females of the same size (ANCOVA, $p< 0.0001$), but the opposite pattern occurred in the Beaufort Sea (ANCOVA, $p< 0.001$), with heavier weights at a given size achieved by immature females rather than mature females. Low sample sizes in the Beaufort Sea and the use of two preservation methods with differential dehydration effects (i.e., frozen versus formalin preservation) likely impacted our estimates of weight-at-age for the Beaufort Sea.

3.2 Mean individual crab weight across survey area

Snow crab were generally much larger in the Beaufort Sea with the largest individuals observed along the outer shelf and slope at depth (Fig. 5). On average, the largest individuals in the Chukchi Sea were found off the Lisburne Peninsula west of Point Hope, Alaska (Fig. 5), with smaller individuals in the southern Chukchi Sea along the coast and on the northern portions of the shelf. This spatial pattern accounted for only 18% of the variability in Chukchi Sea mean individual weight, suggesting considerable small-scale spatial variability of individual snow crab weight. In contrast, about 62% of variability in fourth-root transformed individual weights in the Beaufort Sea were explained by the model due to a well-defined size gradient with smaller crab in nearshore waters and larger crab along the outer shelf and slope at deeper depths.

3.3 Maturity-at-size

For the Chukchi Sea crab, we estimated that 50% of male snow crab reach morphometric maturity at 62 mm CW, based on allometry of CH (Fig. 6A). Female snow crab in the Chukchi Sea achieved 50% morphometric maturity at 46 mm CW based on allometry of the abdominal flap and/or the presence of an egg clutch (Fig. 6B). Size at 50% maturity could not be estimated for the Beaufort Sea because of low sample sizes.

3.4 Fecundity

Mature females collected for fecundity estimation in the Chukchi Sea ranged from 38 to 65 mm CW (Table 2). Mean number of eggs increased with body size (Linear regression, number of eggs = 1,063.7*(CW) – 34,397, $R^2 = 0.50$, Fig. 7) from 7,092 eggs at 38 mm CW to 49,164 eggs at 65 mm CW. Total egg production in the Chukchi Sea was estimated at just over 6.59 billion eggs for 2012.

3.4 Biomass, abundance, and sustainable yield

We estimated total snow crab biomass in both the Chukchi and Beaufort seas (Table 3; Fig. 8) to be substantially higher than previous estimates from the Arctic FMP (Table 4). Our estimate of snow crab biomass in the Beaufort Sea was less than 10% that of Chukchi total biomass (63,577 mt and 746,596 mt, respectively), whereas the Arctic FMP estimated biomass in the Beaufort Sea (29,731 mt) to be 45% of the Chukchi Sea biomass (66,491 mt). All these estimates were considered to be estimates of pristine, or unfished, biomass (Table 3, 4).

We estimated annual harvestable biomass (males ≥ 100 mm CW) to be zero in the Chukchi Sea and 15,894 mt in the Beaufort Sea; therefore, equilibrium biomass and yield values were only computed for the Beaufort Sea. With our updated estimate of the difference between the age-at-maturity and the age intercept of the linear weight-at-age equation (d= 7.0 this study; d= 8.0 in the Arctic FMP, NPFMC 2009), we estimated that yield is maximized at a fishing mortality of F= 0.34 compared to F= 0.36 in the Arctic FMP. Together, these parameters resulted in a biomass at MSY estimate of B_{MSY} = 2,681 mt for the Beaufort Sea, which is approximately twice as high as the Arctic FMP value of B_{MSY} = 1,268 mt (Table 4). Finally, we estimated MSY = 905 mt, about 200% higher than the Arctic FMP-calculated MSY (453 mt, Table 4).

4. Discussion

This study improved our understanding of snow crab biology and population status in the Chukchi and Beaufort seas. Snow crab occurred across the Chukchi shelf, but were found only in a localized portion of the western Beaufort shelf and central Beaufort shelf break and upper slope. Both males and females in the Beaufort Sea reached larger sizes than conspecifics in the Chukchi Sea, even though there was larger overlap in the size range of females between the two seas. Despite size range differences, weight-at-size was similar between the Chukchi and Beaufort seas for males, but not females. Size at 50% maturity and fecundity in the Chukchi Sea were both slightly lower than in other geographic regions (e.g., EBS, Sea of Japan, Gulf of St. Lawrence). Finally, our estimates of total biomass of snow crab in both seas and sustainable yield in the Beaufort Sea only were considerably higher than Arctic FMP estimates (NPFMC 2009), due possibly to increased abundances across multiple years.

4.1 Size distribution and weight-at-size

Snow crab in the Chukchi Sea were smaller (maximum size of 87 mm CW) than conspecifics in other geographic locations, including the Beaufort Sea where the maximum size of 119 mm CW was found for males (this study, also Rand and Logerwell 2011). In other locations, the maximum sizes observed are 162 mm CW in the Gulf of St. Lawrence, Canadian Atlantic (Sainte-Marie et al. 1995, Alunno-Bruscia and Sainte-Marie 1998), 160 mm CW off the coast of western Greenland (Burmeister and Siegstad 2008), and 130 mm CW in the Barents Sea (Agnalt et al. 2011). In the Pacific, maximum reported size in the Sea of Okhotsk is 100 mm CW (Yanagimoto et al. 2004) and ~130 mm CW in the eastern Bering Sea (Turnock and Rugolo 2012). Thus, maximum size of snow crab in the Beaufort Sea, but not the Chukchi Sea, was within the range of maximum sizes observed in other regions. The consistently small sizes observed in the Chukchi Sea suggest that growth may be restricted in this region. One possible reason for restricted growth in the Chukchi Sea is the low bottom temperatures from persistent winter water that occurs on the northeastern shelf for a majority of the year (< -1°C, Weingartner et al. 2005, Grebmeier et al. 2015, Danielson et al. 2017). Temperatures < 1°C can inhibit a positive energy balance in snow crab reared in the lab (Foyle et al. 1989, Thompson and Hawryluk 1990), and may result in skipped molting before terminal molt (Orensanz et al., 2007, Burmeister and Sainte-Marie 2010) or a smaller size-at-terminal molt in field populations (Greenland: Burmeister & Sainte-Marie 2010; Gulf of St. Lawrence: Sainte-Marie & Gilbert 1998; Dawe et al. 2012; Newfoundland: Dawe et al. 2012). Cold temperatures (< -1 °C) also cover the Beaufort shelf, but a marked transition occurs at about 200 m depth, where warmer winter water or Atlantic water (> 0 °C) can persist (Pickart 2004, Crawford et al. 2012). Many of the snow crab in the Beaufort Sea, especially the particularly large individuals, were collected from these deeper, warmer waters, suggesting large crab occur in slightly warmer temperatures in the Beaufort Sea, where they may experience faster growth relative to snow crab in the Chukchi Sea. In contrast, Logerwell et al. (2011) reported a strong association between snow crab and cold waters (< -1.5 °C) on the upper Beaufort Sea slope, but temperature measurements in that study only reached to 140 m, which is above the warmer thermocline that is located below 200 m, where most crab occurred. A majority of the large female crab and the mature males collected in the Beaufort Sea during the present study were found in waters around 0.5 °C around 200 m depth (Bluhm et al. 2015), possibly favoring the warmer Atlantic water conditions where they may grow to a size comparable to that of snow crab in other regions with more moderate temperatures.

4.2 Maturity-at-size

Male size at 50% morphometric maturity in the Chukchi Sea (62 mm CW) was much larger than a previous estimate of 35 mm CW for Chukchi males based on presence of spermatophores (Paul et al. 1997). This discrepancy in maturity-at-size may be due to differences in methodology for determining maturity state – physiological maturity (i.e., development of spermatophores) versus morphometric maturity (i.e., development of large chela). Nevertheless, we cannot rule out that an increase in maturity-at-size has occurred in the region over the last 2 to 3 decades. Comparisons of size at 50% morphometric maturity using CW:CH ratio yield high variability across geographic locations. Males in the EBS and the Barents Sea achieve morphometric maturity at 100 mm CW (Turnock and Rugolo 2012, Dvoretsky and Dvoretsky 2011), but males in the Gulf of St. Lawrence are physiologically mature at 40 mm CW (Sainte-Marie and Hazel 1992); based on spermatophore presence, males in the Barents Sea are mature at 46 mm (Filina and Pavlov 2009), ~ 40 mm CW in the Chukchi Sea (Barber et al. 1994), and 65 mm CW in the eastern Bering Sea (Somerton 1981). We found more agreement in size at 50% maturity for females in the Chukchi Sea. It should be noted that where morphometric and physiological maturity have been measured concurrently, males exhibit physiological maturity at smaller sizes than morphometric maturity (Comeau and Conan 1992, Sainte-Marie et al. 1995).

Females reached 50% maturity at 46 mm CW, identical to a previous estimate in the northeastern Chukchi Sea from over two decades ago (Paul et al. 1997), indicating size at 50% maturity has been conserved in this region. Our estimate was only slightly smaller than size at 50% maturity reported for females from the northern Bering Sea, Gulf of St. Lawrence, and Sea of Japan (50 mm CW for all regions; Ito 1967, Watson 1970, Jewett 1981, Orensanz et al. 2007). The similarity in size at 50% maturity suggests that female reproductive size may be at least partially conserved among some geographic and oceanographic regions, even though phenotypic response to temperature has been observed on a smaller scale in the EBS (between 55 °N to 65 °N, Orensanz et al. 2007). Several investigators suggested that female snow crab tend to be smaller at maturity at the northern limit of their distribution in the Chukchi Sea due to reduced bottom temperatures at northern limits (Jewett 1981, Somerton 1981, Paul et al. 1997). Clinal variation in size at 50% maturity is well established from the southeastern Bering into the northeast Bering and Chukchi seas (Jewett 1981, Stevens and MacIntosh 1986, Paul et al. 1997, Zheng et al. 2001, Ernst et al. 2005, Orensanz et al. 2007), Greenland (Burmeister and Sainte-Marie 2010) and in the Gulf of St. Lawrence, Canada (Sainte-Marie and Gilbert 1998). Our data are consistent with smaller female size at 50% maturity extending into the Chukchi Sea from the Bering Sea.

4.3 Fecundity

Fecundity estimates obtained here were lower than previous estimates obtained from estimates resulting from collections in only the southeastern portion of the Chukchi Sea and in other Arctic regions (Jewett 1981). For example, a 55 mm CW female based on the Chukchi Sea sampling region in our study had a mean fecundity of ~23,000 eggs compared to 28,000 eggs of a female crab at the same size in the southeastern Chukchi Sea (Jewett 1981). Females of the same size would carry about 26,600 eggs in the Canadian Atlantic (Haynes et al. 1976), about 33,300 eggs in the EBS (Jewett 1981), and about 24,000 eggs in the northern Bering Sea (Kolts et al. 2015). Seemingly higher fecundity estimates for female crab of identical size in the southeastern Bering Sea, compared to the Chukchi Sea, may be related to warmer temperatures at lower latitudes as discussed for weight and size above (Orensanz et al. 2007).

The question arises whether female egg production in the Chukchi Sea is sufficient to support the local population or whether this area depends on advection of larvae from the Bering Sea to sustain itself. We estimated total egg production of the U.S. Chukchi Sea crab to be about 6.5 billion eggs in 2012. To approximate local versus advective production, we applied a pelagic larval survival estimate of 22% (Yamamoto et al. 2014) to the 6.5 billion eggs produced; thus, approximately 1.5 billion larvae would presumably recruit and metamorphose into the first benthic instars (instar I; ~3 mm CW for males in the Gulf of St. Lawrence; Comeau et al. 1998). However, the timing of the cruises in the Chukchi Sea over the study period (i.e., August to September) does not align with the assumed recruitment period for the region. For example, Parada et al. (2010) conclude that snow crab benthic settlement in the EBS probably peaks in late summer or early fall (i.e. September to October). The Gulf of St. Lawrence experiences a similar larval release period similar to that in EBS (i.e., May), and settlement occurs in August to late fall (i.e., instar I density increases from August, through October and is highest in December; c.f., Lovrich et al. 1995, Ouellet & Sainte-Marie 2018). Thus, we assume that at least a portion of the observed instar II and III (~5-7 mm CW for males in the Gulf of St. Lawrence, Comeau et al. 1998) include the previous year’s recruits that have molted into larger early benthic instars. The average size frequency distribution of snow crab in the Chukchi Sea in 2012 indicated that 9% of the sampled population (or ~169 million individuals) was ~3-7 mm CW, presumably representing benthic instars I-III, and represents a minimum estimate of the total annual recruitment. Thus, mature females in the Chukchi Sea study region could produce the number of small snow crab we observed in 2012. However, this estimate is admittedly rough given it is based on lab-reared larval survival, observations from a single year, the assumption that all larvae had settled into the benthos by the time of sampling, and that it does not consider variability in the factors influencing larval dispersal nor the fraction of mature females reproducing on a biennial cycle. The degree of larval advection supplying recruits to the Chukchi shelf from adjacent, upstream regions is not currently known (but see larval abundance estimates by Landeira et al. 2017), but advection has been postulated as an important source of crab in the Chukchi and Beaufort seas (Clement et al. 2005, Hu and Wang 2010, Bluhm et al. 2015, Kolts et al. 2015). This notion is supported by the fact that genetically, snow crab in the Bering, Chukchi and Beaufort seas are considered a panmictic population, with strong gene flow among these regions (Hardy et al. 2011, Albrecht et al. 2014). Considerable uncertainty exists in our egg production estimates due to uncertainties about annual versus biennial reproductive cycles, lifetime egg production per female, and larval and early benthic life stage mortality. However, our results suggest that locally sourced recruitment in the Chukchi Sea may be a significant portion of observed crab on the Chukchi shelf. More detailed knowledge of early life history mortality rates of snow crab is necessary to obtain better estimates of the *in-situ* contribution to the Chukchi snow crab population from mature females versus larvae advected from the Bering Sea.

4.4 Biomass, abundance, and sustainable yield

Although our results suggest approximately 242% higher harvestable biomass in the Beaufort Sea compared with previous estimates from the Arctic FMP, remaining uncertainty in many of the life history metrics used for both the Arctic FMP and our calculations warrants the continued use of a conservative management approach (Restrepo et al. 1998, Zheng 2003). Our estimates of total and harvestable biomass in the Chukchi and Beaufort seas were compared with previous biomass estimates in the Arctic FMP, which were calculated on limited data for the two seas (NPFMC 2009). Our revised total biomass estimate was approximately 90% higher than original estimates in the Chukchi Sea, but was also based on a survey area that was 43% larger, which partly explains the higher biomass estimate. Similarly, in the Beaufort Sea, our data set included a 90% larger survey area, and resulted in a total biomass estimate that was approximately twice as high as Arctic FMP estimates. The higher biomass estimate in the Beaufort Sea could, however, not be attributed to the larger survey region, considering that most of the new survey areas in the eastern Beaufort Sea had few or no snow crab (Fig. 8); survey stations used in the Arctic FMP (Logerwell and Rand 2010) covered most of the area in the western Beaufort Sea that had appreciable numbers of snow crab. By including new survey areas to the east, we were able to fully resolve the strong west to east gradient in snow crab abundance and delineate the easternmost extent of snow crab distribution in the Beaufort Sea. Despite the uncertainty associated with biomass estimates, our results suggest that snow crab density (biomass per unit area) in the U.S. Arctic has increased considerably since the early 1990s. Our higher total biomass estimates translated into higher harvestable biomass estimates in the Beaufort Sea, although harvestable biomass in the Chukchi Sea remained zero since no crab larger than 100 mm CW were found. In the Beaufort Sea, our estimate of harvestable biomass was approximately 212% the Arctic FMP estimate, possibly indicating increasing biomass in the region over time. However, crab of marketable size were only observed in the western Beaufort Sea at depths greater than 100 m, far from existing ports and vessel fleets, making commercial harvest of this stock economically less feasible.

We estimated higher densities in the Chukchi Sea (387,691 individuals km^{-2}) than a previous estimate that used Arctic Eis EBT trawl data only (212,000 individuals km^{-2}, Goddard et al. 2012). Over the entire U.S. Chukchi Sea area, our total abundance (56 million individuals) was sizably larger than the 4 million individuals estimated in Goddard et al. (2012), due to the high numbers of small crab collected during cruises employing the PSBT in the present study. Abundance was low in the Beaufort Sea, with an estimated 46 individuals km^{-2}, and a total of 2.3 million individuals for the entire survey region. In comparison, a previous survey conducted solely in the western Beaufort Sea found 99,600 individuals km^{-2} (Rand and Logerwell 2011); no estimate for total survey area was available for that earlier study.

Our results provide an updated estimate of the difference between the age-at-maturity and the age intercept of the linear weight-at-age equation (*d*) that was derived from new, region-specific data on Arctic snow crab. Harvestable biomass estimates changed considerably (Table 4), but these changes were related primarily to the substantial increase in estimated pristine or unfished biomass, rather than to changes in parameter estimates. The much higher estimates of total biomass in the Chukchi Sea, and of both total and harvestable biomass in the Beaufort Sea, compared to the FMP estimates, resulted from a combination of improved spatial coverage and higher densities of snow crab in the recent period. Due to the remoteness and relatively low density of large snow crab on the Beaufort Sea slope, our updated estimates do not warrant a change to the Arctic FMP with respect to the “Optimum Yield” specified for snow crab, which is currently set to zero based in part on cost considerations (NPFMC 2009).

4.5 Conclusions

Our results are intended to inform the management of the Arctic snow crab stock off the coast of Alaska and to expand our understanding of Arctic snow crab life history parameters and distribution trends in light of potential future fisheries or other, non-fishing activities. Most population parameters we investigated in this study were reasonable comparable to those in other geographic regions where snow crab occur. We found generally similar weight-at-size rates in snow crab between sexes and seas. Both size at 50% maturity and fecundity estimates were within similar ranges as for snow crab occurring in other geographic localities. Our new estimates of biomass and sustainable yield update existing Arctic FMP estimates with results from recent surveys and region-specific life history parameters. Estimates of fishery reference points may be further improved with inclusion of molting probabilities, size-at-age data, and region-specific natural mortality estimates, should those become available in the future. Our estimate of fecundity could be improved if information becomes available regarding the percentage of females on an annual versus biennial reproductive schedule. Ultimately, the results of the present study support continued precautionary management of U.S. Arctic snow crab stocks, which does not allow for commercial harvest at this time. Continued monitoring with the intent of augmenting the temporal coverage of snow crab size frequency distributions, biomass, and abundance, as well as investigations into the larval dispersal and migratory connectivity of snow crab occurring in the Bering, Chukchi, and Beaufort regions, will greatly facilitate improved management of snow crab as a potential future fishery resource.

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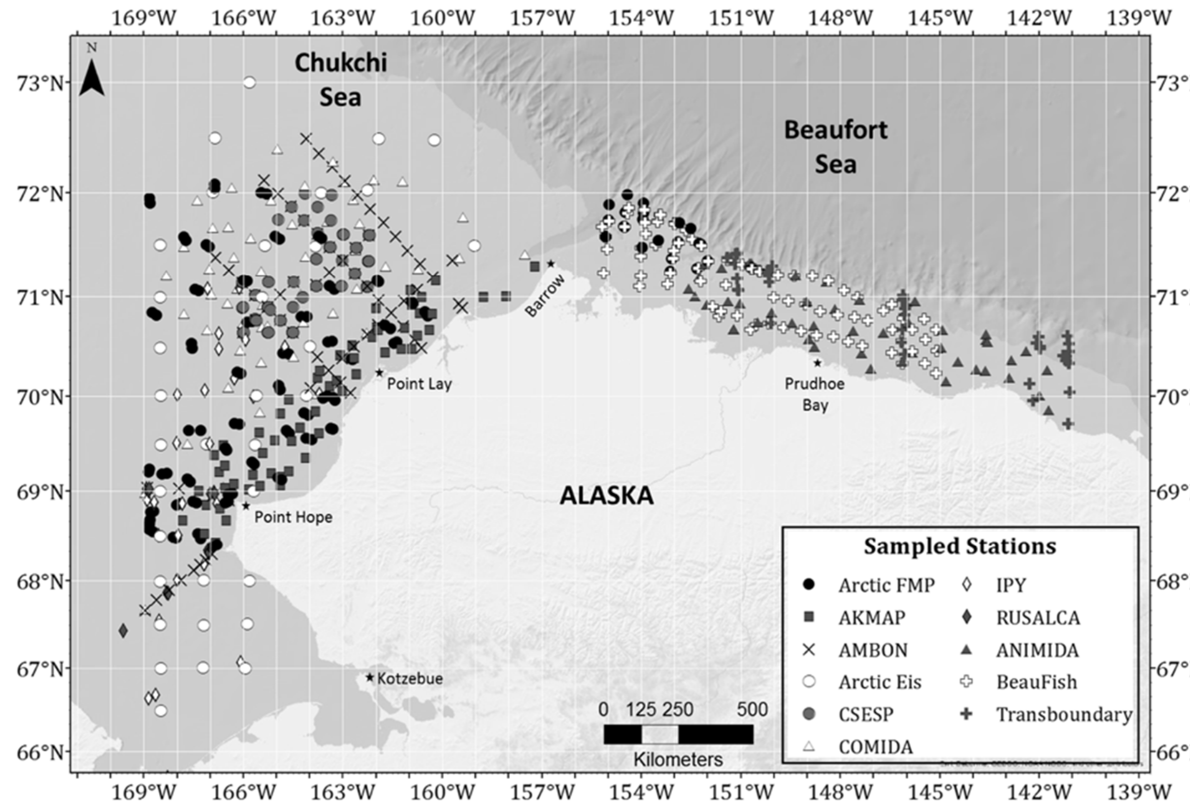

Figure 1. Stations sampled on the Alaska Chukchi and Beaufort Sea shelves from 2004 to 2017. Stations denoted as black circle data points occurring in the Chukchi and Beaufort seas are stations that contributed to biomass estimates in the Arctic Fishery Management Plan (Barber et al. 1994, NPFMC 2009, Rand and Logerwell 2011).

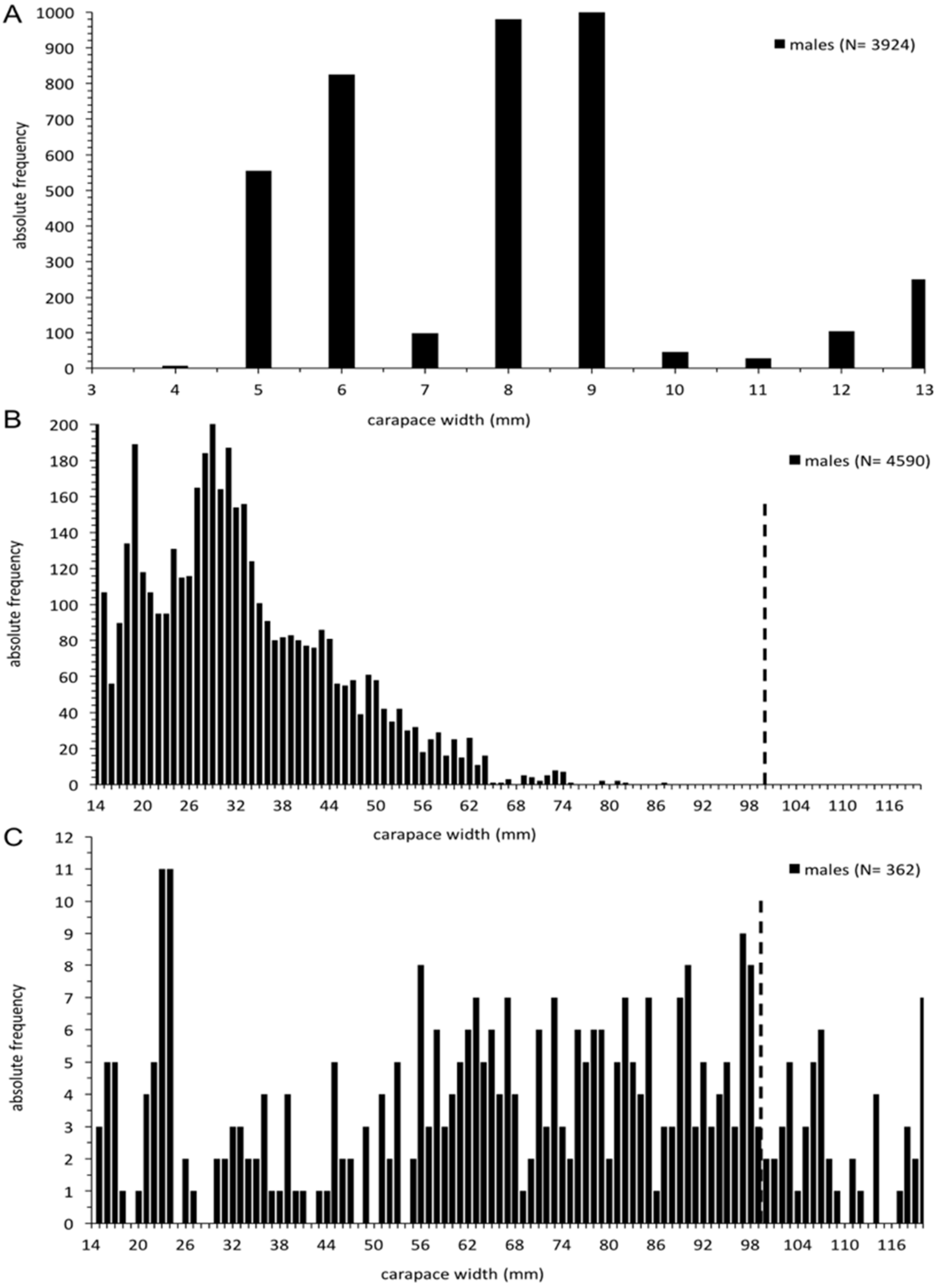

Figure 2. Size frequency distributions for males (A) ≤ 13 mm CW in the Chukchi Sea, (B) >13 mm CW in the Chukchi Sea collected from 2004 to 2015, and (C) >13 mm CW collected in the Beaufort Sea from 2008 to 2015. Note the different scales of the y-axes. Black dashed line indicates the minimum marketable size (≥ 100 mm CW) applicable for the Bering Sea commercial snow crab fishery.

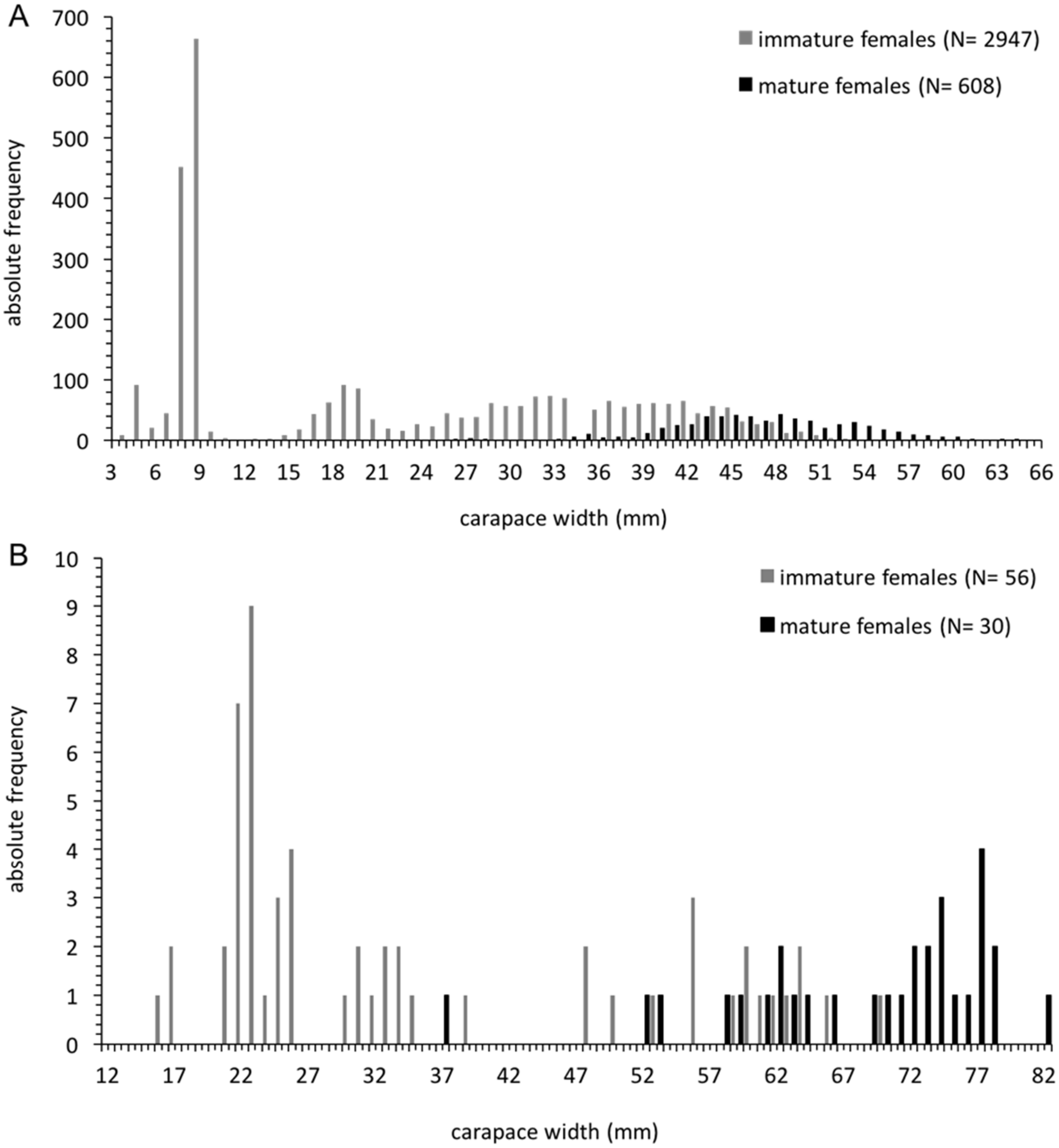

Figure 3. Size frequency distributions for immature and mature females (A) in the Chukchi Sea collected from 2004 to 2015, and (B) immature and mature females collected in the Beaufort Sea from 2008 to 2015. Note the different scales of the y-axes.

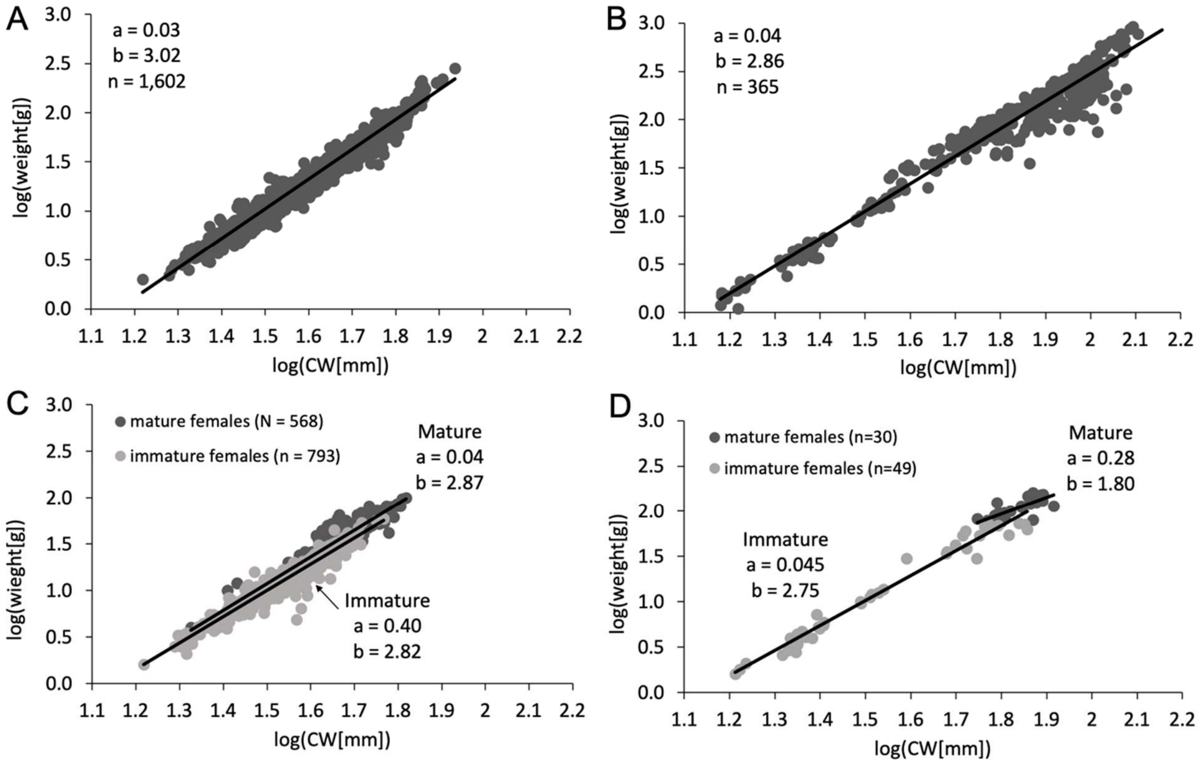

Figure 4. Weight-at-size regressions of A) Chukchi Sea males (weight(g)= 3.0*CW - 3.5), B) Beaufort Sea males (weight(g)= 2.8*CW - 3.2), C) Chukchi immature (weight(g)= 2.8*CW - 3.1) and mature females (weight(g)= 2.8*CW - 3.2), and D) Beaufort immature (weight(g)= 2.8*CW - 3.1) and mature females (weight(g)= 2.3*CW - 2.3) (estimated from snow crabs collected from 2004 to 2015). Weight-at-size parameters (*a* = intercept and *b* = slope) and sample sizes are presented in the respective figures.

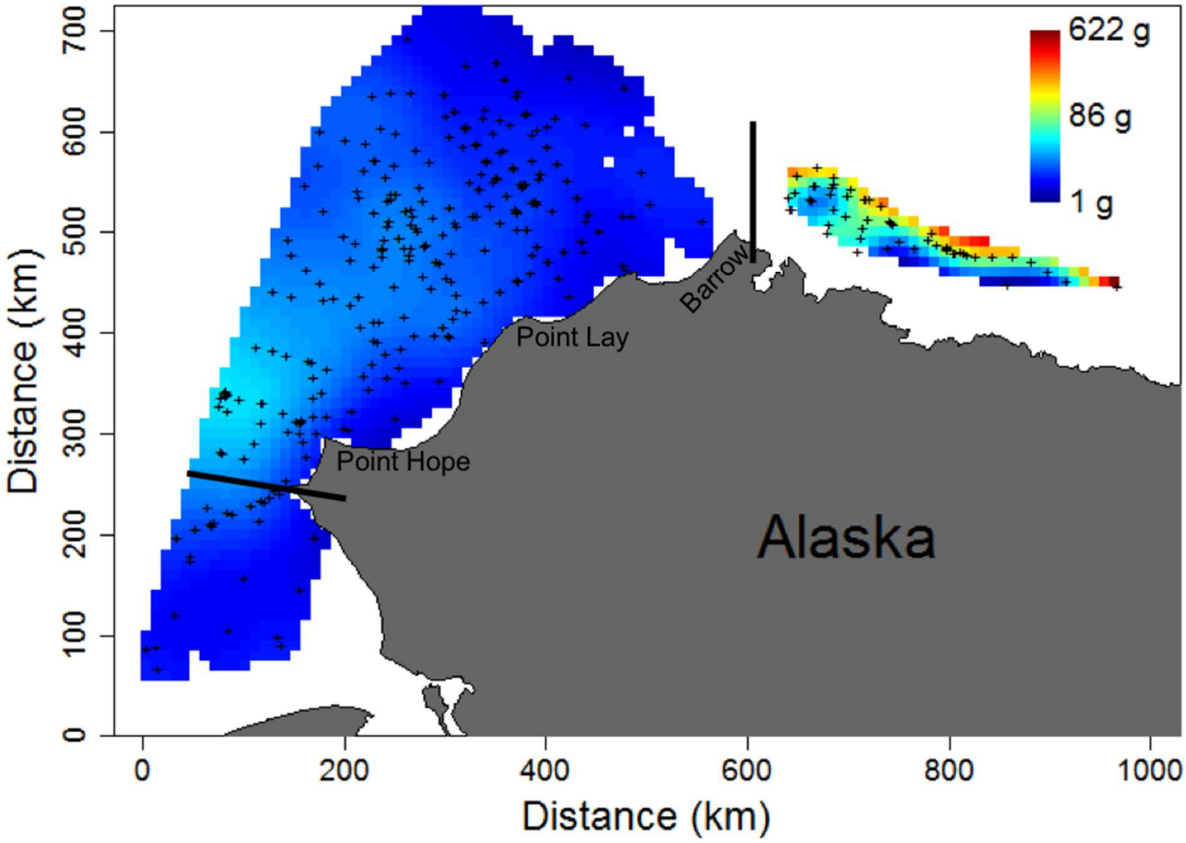

Figure 5. Predicted individual mean snow crab weight (g, log-scale) in the Chukchi and Beaufort seas based on thin-plate regression splines fit separately to the Chukchi Sea ($R^2 = 18\%$) and Beaufort Sea ($R^2 = 62\%$), estimated from PSBT CPUE data pooled over multiple surveys conducted between 2004 and 2015. Crosses denote all stations where snow crab weights were collected.

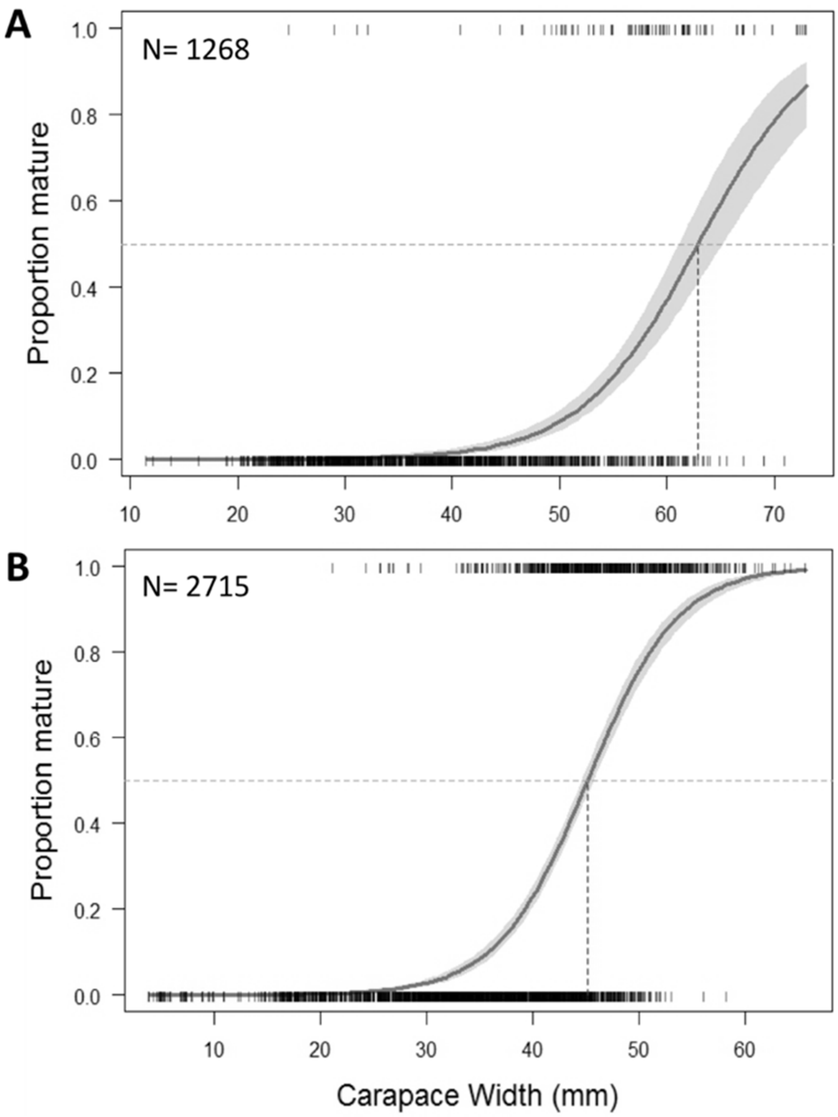

Figure 6. Size at 50% morphometric maturity (dark gray solid lines) with 95% confidence intervals (light gray shaded areas) for (A) males and (B) females estimated from snow crab collected in the Chukchi Sea. Size at which 50% of all crab are morphometrically mature is denoted at the intersection of the gray dashed lines.

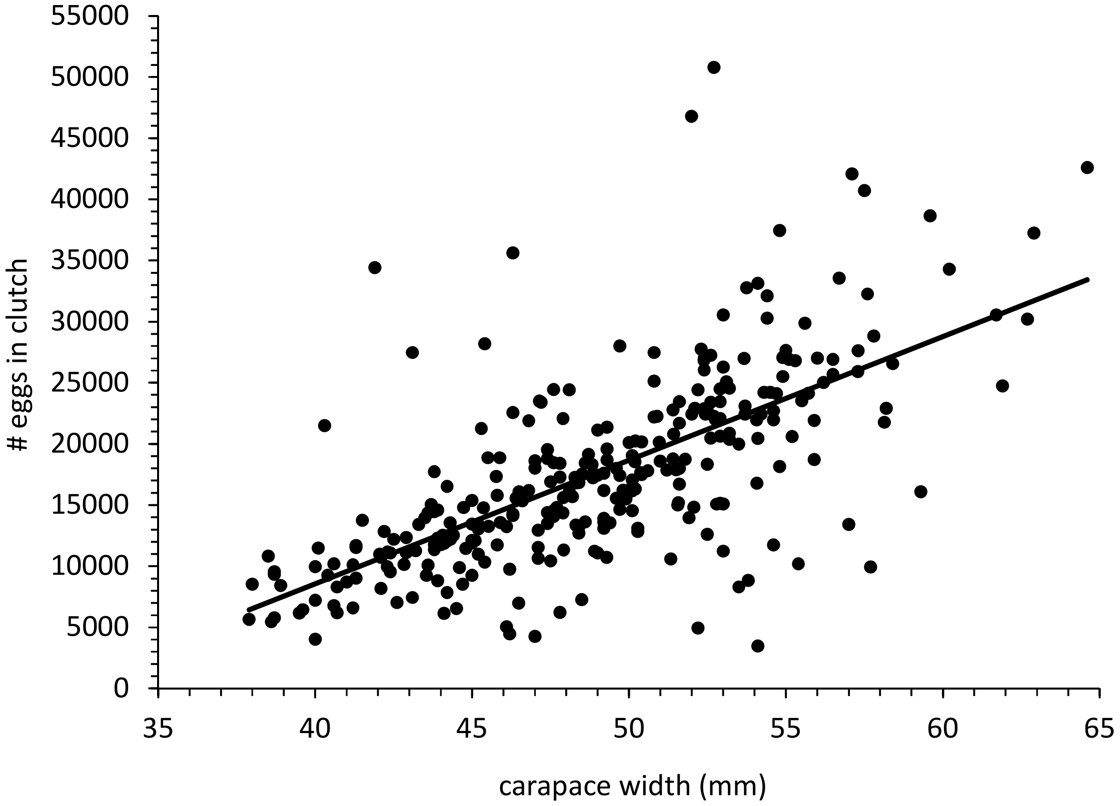

Figure 7. Fecundity as number of eggs plotted against body size (carapace width) per mature female snow crab collected from the Chukchi Sea from 2009 to 2012. Number of eggs in a clutch = 2.9*CW - 1.61, $R^2 = 0.50$.

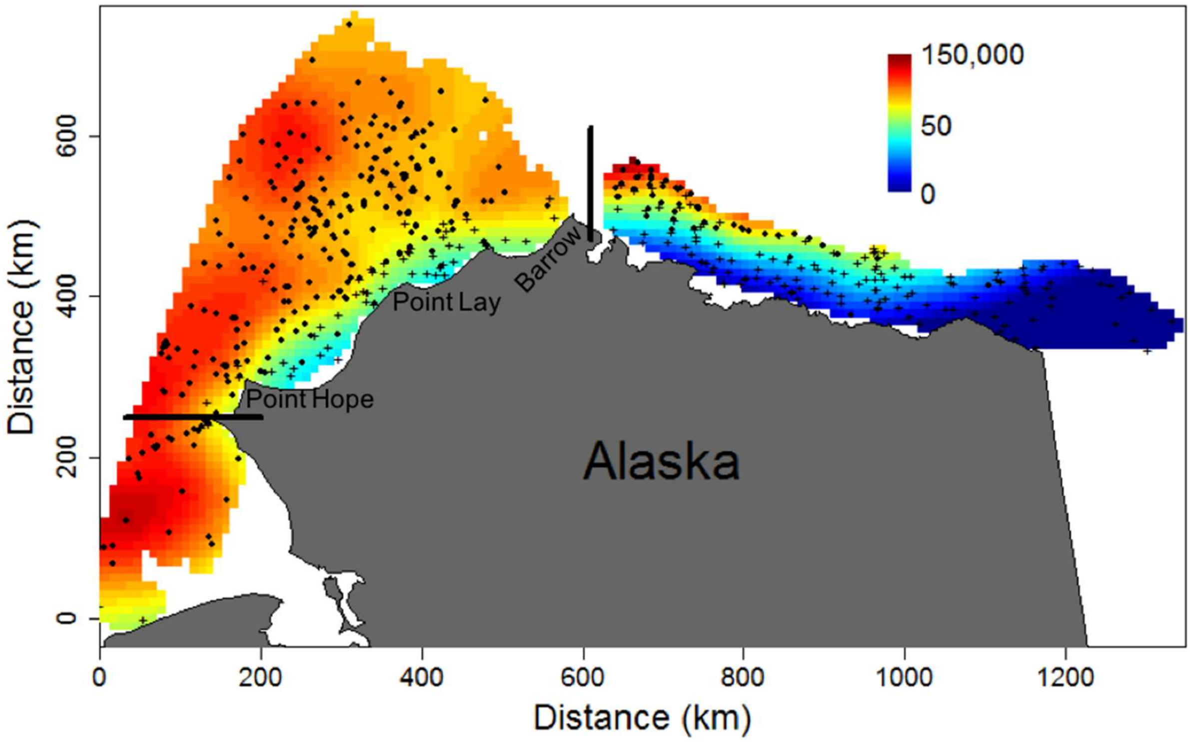

Figure 8. Predicted mean snow crab biomass (kg km^{-2}, log-scale) in the Chukchi and Beaufort seas, estimated from PSBT CPUE data pooled over multiple surveys conducted between 2004 and 2017. Symbols show hauls with (filled circle) and without (cross) snow crab. Black lines delineate geographic areas over which total biomass was estimated (i.e., southern and northern Chukchi Sea, Beaufort Sea; Table 1).

Table 1. Cruise data showing the timing of sampling, project name, gear type used, and data provided for the current study. PSBT= plumb staff beam trawl, EBT= Nor'Eastern bottom trawl. Major funding sources indicated by superscripts.

Month/ Year	**Project**	**Gear Type**	**# hauls (by gear type)**	**# crab collected**	**Data Provided**
Chukchi Sea					
Aug 2004	RUSALCA-1 [a]	PSBT	4	58	Biomass, abundance, size frequency
Aug 2007	Oscar Dyson [a]	PSBT	11	-	Biomass, abundance
Aug 2008	Oshoru Maru IPY [b]	PSBT	15	-	Biomass, abundance
Aug 2009	RUSALCA-2 [a]	PSBT	3	1,298	Biomass, abundance, size frequency, fecundity
Aug 2009	COMIDA [c]	PSBT	30	-	Biomass, abundance
Aug 2010	COMIDA [c]	PSBT	23	290	Biomass, abundance, size frequency, fecundity
Sept 2010	CSESP [d]	PSBT	70	479	Biomass, abundance, size frequency
Aug-Sept 2010	AKMAP [e]	PSBT	30	505	Biomass, abundance, size frequency
Sept 2011	AKMAP [e]	PSBT	28	49	Biomass, abundance, size frequency
Aug 2012	RUSALCA-3 [a]	PSBT	4	1,766	Biomass, abundance, size frequency, fecundity
Aug-Sept 2012	Arctic Eis [c]	PSBT, EBT	40, 71	493	Biomass, abundance, size frequency, fecundity, maturity-at-size
Aug-Sept 2015	AMBON [a,c,d]	PSBT	67	6,975	Biomass, abundance, size frequency
Aug 2017	AMBON [a,c,d, g]	PSBT	81	234	Biomass, abundance, size frequency
Beaufort Sea					

Aug-Sept 2008	Western Beaufort Fish Survey [c]	PSBT	21	334	Biomass, abundance
Aug-Sept 2011	BeauFish Survey [c,f]	PSBT	83	64	Biomass, abundance, size frequency
Sept 2012	Transboundary [c]	PSBT	18	50	Biomass, abundance, size frequency
Aug-Sept 2013	Transboundary [c]	PSBT	42	1	Biomass, abundance, size frequency
Aug-Sept 2014	Transboundary [c]	PSBT	10	-	Biomass, abundance
Aug 2014	ANIMIDA [c]	PSBT	29	3	Biomass, abundance, size frequency
Aug 2015	ANIMIDA [c]	PSBT	17	33	Biomass, abundance, size frequency

Major funding sources: [a] NOAA: National Oceanographic and Atmospheric Administration; [b] Japanese Funding, [c] BOEM: Bureau of Ocean Energy Management (in 2008 as Minerals Management Service), [d] Oil Industry (Shell Oil, Conoco Phillips, Statoil), [e] ADEC: Alaska Department of Environmental Conservation, and CIAP: Coastal Impact Assistance Program, [f] CMI: Coastal Marine Institute, g: National Science Foundation.

Table 2. Mean eggs per clutch scaled to snow crab body size (carapace width, CW) and proportion of female snow crabs at each CW that are mature in the Chukchi Sea for the range of mature females observed in this region (38 to 65 mm CW).

CW (mm)	mean # eggs per clutch	proportion mature
38	7,092	0.19
39	8,231	0.22
40	9,505	0.25
41	8,917	0.29
42	13,258	0.33
43	12,489	0.37
44	12,307	0.41
45	13,188	0.46
46	14,765	0.50
47	16,167	0.55
48	15,592	0.59
49	16,339	0.63
50	17,387	0.67
51	20,363	0.71
52	21,282	0.75
53	22,380	0.78
54	21,700	0.81
55	23,223	0.83
56	24,441	0.86
57	27,881	0.88
58	26,138	0.90
59	16,105	0.91
60	36,477	0.93
61	34,044	0.94
62	31,611	0.94
63	33,720	0.95
64	31,923	0.96
65	42,597	1.00

Table 3. Biomass estimates (metric tons, mt) with 95% lower (LCI) and upper (UCI) confidence intervals over different portions of the survey area. Northern and southern Chukchi Sea correspond to areas north or south of Point Hope, Alaska, USA (see Fig. 1 for reference).

Region	**Area (km^2)**	**Estimate (mt)**	**LCI (mt)**	**UCI (mt)**
Chukchi Sea (total)	172,000	746,596	442,139	1,591,622
Chukchi Sea (North)	138,000	411,357	252,351	814,453
Chukchi Sea (South)	34,000	335,239	163,584	880,476
Beaufort Sea	64,400	63,577	31,878	167,613

Table 4. Estimates of total and harvestable biomass in the Chukchi and Beaufort seas as determined in the Arctic FMP (NPFMC 2009) and based on the revised estimates (this study) for snow crabs calculated on Arctic-specific population parameters. B_0= pristine or unfished biomass, F_{MSY}= Fishing mortality at maximum sustainable yield (MSY), B_{MSY}= biomass at MSY, mt= metric tons.

Parameter	**Arctic FMP**	**This study**
Total B_0 (Chukchi Sea)	66,491 mt	746,596 mt
Total B_0 (Beaufort Sea)	29,731 mt	63,577 mt
Harvestable B_0 (Chukchi Sea)	0 mt	0 mt
Harvestable B_0 (Beaufort Sea)	6,571 mt	15,894 mt
F_{MSY}	0.36	0.34
B_{MSY}	1,268 mt	2,681 mt
MSY	453 mt	905 mt
B_{MSY}/B_0	0.19	0.17
MSY/B_0	0.06	0.06