



Estimation of annual, time-varying natural mortality and survival for Eastern Bering Sea snow crab (*Chionoecetes opilio*) with state-space population models

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ABSTRACT

Sex-specific, state-space population models with size and stage structure and fit to survey and fishery data were developed for the eastern Bering Sea (EBS) snow crab for the years 1982–2017. Motivation for model development was to estimate population dynamics by shell condition for female crabs; estimate sex-specific annual, time-varying natural mortality rates; and explore in general the feasibility of state space modeling for EBS snow crab. Model fits were very good and mean natural mortality estimates agreed with previous studies but several quite high and/or quite low annual natural mortality values were estimated for both sexes. Estimated mean female natural mortality was 0.49 yr^{-1} (s.d. = 0.01) with annual values from 0.04 yr^{-1} to 3.34 yr^{-1} . Estimated mean male natural mortality was 0.36 yr^{-1} (s.d. = 0.07) with annual values from 0.03 yr^{-1} to 0.91 yr^{-1} . Episodic high and low annual natural mortality estimates indicate potential model overfitting which an autoregressive or random walk estimation framework for natural mortality may address. We consider the models as proof-of-concept estimation frameworks and their results preliminary. After further refinement and testing, they could be a complementary approach to ongoing stock assessment modeling or prototypes for state-space assessment models. Additional process variability, such as for growth and maturation, can be incorporated in future work. Abundance estimates by mature female shell condition makes feasible estimation of annual and biennial spawner abundances, necessary for accurate egg production estimation. State-space population dynamics models of other *Chionoecetes* populations with both size and stage-based data (e.g., maturity status or shell condition) can be developed utilizing this study's modeling framework.

1. Introduction

Development of statistical population models for snow crab (*Chionoecetes opilio*) and other congeneric *Chionoecetes* species have been ongoing since the early 1990s. One of the first such efforts was the change-in-ratio model of Dawe et al. (1993) which estimated population sizes of large male abundances in the Western North Atlantic (WNA). Zheng et al. (1998), using the size-based modeling framework of Sullivan (1992) and Zheng et al. (1995), developed sex-specific, size and stage-based assessment models for Bristol Bay Tanner crab (*C. bairdi*) in the eastern Bering Sea (EBS) that are the forerunners to the current EBS stock assessment models for snow crab and Tanner crab. Zheng (2003) separately modeled males and mature females to estimate sex-specific natural mortality rates. Drouineau et al. (2013) expanded the female model of Zheng (2003) by including carapace width data for estimation of mature female natural mortality for a WNA snow crab

population.

Three important features of the *Chionoecetes* genus require special attention for population modeling: determinate growth due to a terminal molt (Conan and Comeau, 1986); strong sexual growth and size dimorphism (males larger than females) (Comeau et al., 1998); and, the absence of age data. (For this study, using EBS convention, we categorize all pre-terminally molted crabs as “immature” and all post-terminally molted crabs as “mature.”). Post-terminal molt, mature males and mature females will survive a number of years though growth has ceased and the carapace is not replaced. Lack of age data, due to lack of retained body parts or tissues containing age-related information, requires size-based population modeling approaches. The large sexual size dimorphism, in addition to implying distinct sex-specific growth and maturation, results in females having no commercial value in some regions. In the EBS, snow and Tanner crab fisheries only target and retain large males, and females experience negligible fishing

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mortality; thus, fishery-dependent data contain no useful information for female population dynamics.

While currently no empirical method can provide an absolute age estimate for *Chionoecetes* species, carapace shell condition provides a rough proxy for the elapsed time since terminal molt (Fonseca et al., 2008). Annually molting immature crabs and recently terminally-molted crabs have mostly unblemished, undegraded carapaces free of epibiont growth. The carapaces of mature, post-terminal molt crabs become increasingly degraded with elapsed time since terminal molt, and are marked by noticeable change in color, the presence of epibiont growth, and shell damage. Crabs are subjectively classified as newshell and oldshell in data collected by the annual National Marine Fisheries Service (NMFS) EBS summer bottom trawl survey; oldshell crabs are assumed to be at least one year past terminal molt and all other crabs are considered newshell (Otto, 1998).

Given that shell condition is a subjective determination, a potential for misclassification exists and appears to differ between sexes in the EBS due to the respective timing of the molt-to-maturity and when crabs are sampled by the summer survey (Ernst et al., 2005). Males and females undergo the terminal molt at different times during the year: females during December–March; and males March–June (Ernst et al., 2005; Orensanz et al., 2007; Sainte-Marie et al., 2008). Crabs of either sex that terminally molted in the year prior to the summer survey are thought easily recognizable as newshell. The timing of terminal molting appears to create a clear distinction between newshell and oldshell females, with females terminally molting in the winter prior to the survey having clean, unblemished shells at the time of the survey, but then having categorically darker, more blemished shells the following year. Female shell condition classification is considered straightforward during spring and summer sampling (Ernst et al., 2005; Drouineau et al., 2013).

Female EBS snow crab have distinct spatial structure due to ontogenetic cross-shelf migration with younger, newshell crabs inshore and oldshell crabs further offshore (Somerton, 1981; Zheng et al., 2001). Due to a persistent, strong cross-shelf bottom temperature gradient – colder inshore, warmer offshore – this spatial structure results in newshell and oldshell occupying generally distinct thermal habitats (Murphy et al., 2017). These different thermal habitats have strong consequences on female egg production due to the frequency of reproductive cycle being a function of bottom temperature with annual spawning in warmer waters and biennial spawning in colder waters (Rugolo et al., 2005; Murphy et al., 2017). Additionally, newshell mature females and oldshell mature females have different size-specific fecundity (Sainte-Marie, 1993). Thus, population estimates for female EBS snow crab by shell condition (e.g., younger mature crabs vs. older mature crabs) is necessary for accurate estimation of egg production (Murphy et al., 2017).

The EBS snow crab fishery only retains large males and targets large newshell males, due to higher commercial value (NPFMC, 2000); thus, population estimates for males by shell condition is also of interest. However, the relationship between male shell condition classification and elapsed time since terminal molt is less clear than for females. Males that terminally molted in the spring prior to the survey year, may have relatively cleaner shells compared to females that also molted the previous year as less time has elapsed since the terminal molt. In the EBS snow crab survey data, it is believed that males with carapaces still in excellent condition despite having terminally molted the year previous to the survey year, may be misclassified as newshell males. Unrealistically high estimates of EBS mature male natural mortality based on male shell condition data (Otto, 1998; Zheng, 2003) support the arguments that misclassification occurs for EBS males as this would lead to inflated newshell abundances, lower oldshell abundances, and high natural mortality estimates. As a consequence, male shell condition appears a poor proxy for elapsed time since terminal molt for EBS newshell males. Additionally, a longitudinal tagging study of terminally-molted males in the WNA showed that males that terminally

molted the previous calendar year can be misclassified as newshell even by expert biologists during spring and summer sampling (Fonseca et al., 2008).

In this study then, sex-specific state-space models are developed where shell condition is used as a population stage for females but not for males. State-space models, also called random-effects or hierarchical models (Maunder and Deriso, 2011), allow for estimation of process variability (e.g., time-varying natural mortality) in population dynamics models. Such approach differs from typical assessment models where vital rates such as natural mortality are either fixed at an assumed value or a time-invariant estimate is used for the model time period (e.g., Suuwaliki and Turnock, 2016). The primary objectives of this study are i) to implement a state-space modeling framework to estimate annual, time-varying natural mortality; ii) to integrate shell condition as a covariate for female EBS snow crab population dynamics; and iii) assess the general utility of state-space population modeling for the EBS snow crab.

2. Data and methods

2.1. Survey overview and data

Survey data used in this study were from the annual NMFS EBS bottom trawl survey, the principal resource survey for crab and groundfish and conducted annually since the 1970s (Daly et al., 2016). A detailed overview of current methodology and history is provided in Daly et al. (2016). In this study, only data from 1982 to 2017 were used; while earlier data were available, the survey covered much less area prior to 1980 and changed gears in 1982. The survey gear has remained relatively unchanged since 1982; and except for a small change in 1987–1988, so has survey coverage. No experimental data or survey data analysis has indicated that survey catchability has changed during the model time period. Survey stations are distributed using a lattice design on a 20 nmi × 20 nmi grid in depths from 20 m to 200 m across the EBS shelf, and a 30 min trawl occurs at the center of each station; hauls are either sampled whole or subsampled. Relevant biological sampling of snow crab includes carapace width, shell condition as an ordinal value: 1 is for just-molted with soft carapace and newshell condition; 2 is for recently molted (presumably within the year) newshell crabs; and values 3, 4, and 5 are for oldshell crabs with increasingly degraded carapaces and presumably at least one year past their terminal molt. For females, maturity status (immature or mature) is easily classified based on distinct abdomen morphology. Chela heights are measured on a subset of male snow crabs for maturation data; mature males have enlarged chelae, and the allometric relationship between the chela and carapace width determines whether it is assigned immature or mature status.

2.1.1. Biomass and size composition data

Annual biomass values and size compositions were estimated for three population stages for females (immature, newshell mature, and oldshell mature) and for two male stages (immature and mature). Biomass and abundance estimates and associated variances were calculated based on stratified, area swept estimates as described by Kimura and Somerton (2006). Membership of each female sampled on the survey to one of the three population stages can be explicitly inferred from the survey data. Annual abundances by 5 mm size classes were used to calculate size composition data for each female population category.

Biomass and size composition estimates for immature and mature males required estimates of the proportion mature by 5 mm size class among newshell males; following the EBS convention, all oldshell males were assumed mature. Chela height data from 1989 (the initial year of systematic collection on the survey) through 2017 were used to calculate a single time-averaged estimate of the proportion mature for each size class. Each male sampled for chela height data was weighted

by the sampling factor of the derivative haul using the inverse of the proportion of haul sampled (Zheng, 2008) and classified as mature based on the chela height to carapace width ratio (≥ 0.20), or as immature (Daly et al., 2016). The proportion mature for a given size bin was the sum of the weighted values for males classified as mature divided by the weighted values for all males sampled in that size bin. Estimates of proportion mature were then applied to size-specific newshell biomasses at the station-level to partition station-level newshell biomass into immature and mature components; then, annual population level biomasses for each male stage were calculated following Kimura and Somerton (2006).

2.2. Catch data

Retained catch data (males only) were taken from the annual stock assessment report (Szuwalski and Turnock, 2016).

2.3. Population model

2.3.1. Overview

The sex-specific models developed were stage and size-based. The female model had three life-history stages: newshell immature (immature, hereafter), newshell mature, and oldshell mature stages. Female immature crabs annually molted and either remained as immature crabs or terminally molted and transitioned to the newshell mature category. Newshell mature crab transitioned to the oldshell mature category after one year. Annual recruitment was to the immature category. The male model did not consider shell condition and had two life-history stages: immature and mature. Immature males annually molted and remained immature after the annual molt or transitioned to the mature category. Annual molting for immature crabs with no skip-molting was assumed for both sexes, following growth assumptions in the EBS snow crab stock assessment (Szuwalski and Turnock, 2016). Annual natural mortality differs by sex but is the same for all crabs for each sex.

The models followed an annual time step and the start of the model year was the time of the summer survey. The female model had 10 size classes: 30–34 mm to 75–79 mm; the male model had 20 size classes: 35–39 mm to 130–134 mm. The minimum sizes were chosen based on survey data (survey catch of very small crabs is low and noisy), and to ensure that the sizes correspond to the adolescent growth phase rather than the immature growth phase, simplifying growth dynamics modeling (Sainte-Marie et al., 1995; Comeau et al., 1998; Somerton et al., 2013; Kotwicki et al., 2017). Given that negligible amounts of bycatch occur for female snow crab and immature males in the EBS (Otto, 1998; Zheng, 2003; Gaeuman, 2014; Szuwalski and Turnock, 2016), annual survival for females and immature males was considered equivalent to survival of natural mortality.

2.3.2. Population dynamics

Matrix notation is used to describe the population dynamics; matrices have dimensions $n_j \times n_j$, where n_j is the number of size classes and vectors are $n_j \times 1$ column matrices. Subscripts are i , immature; m , mature; n , newshell mature; o , oldshell mature; j , size class; k , sex; and y , year.

2.3.2.1. Female population dynamics. Population dynamics for immature female crabs ($k = \text{female}$) are

$$\mathbf{N}_{k,i,y+1} = (\mathbf{I} - \mathbf{Q}_k) \mathbf{G}_k \mathbf{S}_{k,y} \mathbf{N}_{k,i,y} + \mathbf{R}_{k,y+1}, \quad (1)$$

where \mathbf{N} is a vector of abundances; \mathbf{S} is a diagonal matrix of annual survival values; \mathbf{G} is a size-transition matrix; \mathbf{Q} is a diagonal matrix of time-invariant, size-specific post-molt maturation probabilities; \mathbf{I} is the identity matrix; and \mathbf{R} is a vector of size-specific recruit abundances. Abundances of newshell mature crabs by sex, $\mathbf{N}_{k,m}$, are calculated from the abundances of immature crabs that survived the previous year and

then molted to maturity (terminally-molted):

$$\mathbf{N}_{k,n,y+1} = \mathbf{Q}_k \mathbf{G}_k \mathbf{S}_{k,y} \mathbf{N}_{k,i,y}. \quad (2)$$

Oldshell abundances by sex, $\mathbf{N}_{k,o}$, are calculated from oldshell and newshell mature crabs that survived the previous year,

$$\mathbf{N}_{k,o,y+1} = \mathbf{S}_{k,y} [\mathbf{N}_{k,o,y} + \mathbf{N}_{k,n,y}]. \quad (3)$$

2.3.2.2. Male population dynamics. Immature male dynamics are as described in Eq. (1) with $k = \text{male}$ and with the survival matrix indexed by maturity stage. Mature male dynamics are

$$\mathbf{N}_{k,m,y+1} = \mathbf{Q}_k \mathbf{G}_k \mathbf{S}_{k,i,y} \mathbf{N}_{k,i,y} + \mathbf{S}_{k,m,y} \mathbf{N}_{k,m,y}, \quad (4)$$

where $\mathbf{N}_{k,m}$ is a vector of mature abundances and other notation is same as in Section 2.3.2.1 for female dynamics.

2.3.3. Maturation

Diagonal elements of \mathbf{Q}_k are time-invariant sex and size-specific post-molt maturation probabilities:

$$Q_{k,j,j} = \gamma_{k,j}, \quad (5)$$

where $\gamma_{k,j}$ is the estimated post-molt maturation probability for size class j of sex k .

2.3.4. Natural mortality, fishing mortality, and annual survival

For female and immature male crabs, survival is a function of natural mortality (discard mortality from directed fisheries and bycatch from other fisheries are considered negligible). For mature males, survival is a function of natural and fishing mortality.

2.3.4.1. Natural mortality. Annual natural mortality for sex k is

$$M_{k,y} = \bar{M}_k \exp(\sigma_{\omega,k} \omega_{k,y} - 0.5\sigma_{\omega,k}^2), \quad (6)$$

where $\omega_{k,y}$ is an estimated annual random effect from a standard normal distribution; $\sigma_{\omega,k}$ is the estimated standard deviation of the distribution of annual random effects; \bar{M}_k is the estimated expected value of $M_{k,y}$; and $0.5\sigma_{\omega,k}^2$ is the lognormal bias correction factor.

2.3.4.2. Annual survival. Annual female survival is equal for all size classes and stages and diagonal elements of $\mathbf{S}_{k,y}$ ($k = \text{female}$) are

$$S_{k,y,j,j} = \exp(-M_{k,y}). \quad (7)$$

Annual immature male survival, $S_{k,i,y,j,j}$, is as described for females with $k = \text{male}$. For mature males, diagonal elements of $\mathbf{S}_{k,m,y}$ are

$$S_{k,m,y,j,j} = \exp(-(M_{k,y} + F_{j,y})), \quad (8)$$

where $k = \text{male}$ and $F_{j,y}$ is an annual, size-specific fishing mortality rate.

2.3.5. Catch, exploitation rate, and fishing mortality

A simplified fishing mortality framework was implemented that modeled only the retained catch in the directed fishery, which comprises the vast majority of fishery removals and fishing mortality for snow crab (Szuwalski and Turnock, 2016). Discard mortality of smaller crabs by the directed fishery, bycatch from non-directed fisheries, and the pulse dynamics of the directed fishery (which typically occurs over a few winter months) were not modeled. The retained catch was assumed comprised only of mature males (Otto, 1998; NPFMC, 2000). The vector of size-specific catches of males in year y , $\mathbf{C}_{k,y}$, is calculated as

$$\mathbf{C}_{k,y} = \mathbf{U}_{k,y} (\mathbf{I} - \mathbf{S}_{k,y}) \mathbf{N}_{k,m,y}, \quad (9)$$

where $k = \text{male}$ and the diagonal elements of matrix $\mathbf{U}_{k,y}$ are annual size-specific exploitation rates of mature males,

$$U_{k,y,j} = \frac{F_{j,y}}{F_{j,y} + M_{k,y}} \quad (10)$$

Values of annual fishing mortality on mature males are calculated as

$$F_{j,y} = v_j \dot{F}_y, \quad (11)$$

where v_j is the time-invariant fishery selectivity value for size class j ; and \dot{F}_y is the fully selected fishing mortality for year y . Values of v_j are calculated as a logistic function, $v_j = [1 + \exp(e_1(l_j - e_2))]^{-1}$, where l_j is the mid-point of size class j ; e_1 is the estimated slope of the logistic curve; and e_2 is the estimated size at 50% selectivity. Annual values of \dot{F}_y are calculated as

$$\dot{F}_y = \bar{F} \exp(\sigma_F \omega_{F,y} - 0.5\sigma_F^2), \quad (12)$$

where \bar{F} is the expected value of \dot{F}_y ; $\omega_{F,y}$ is an estimated annual fishing mortality random effect from a standard normal distribution; σ_F is the estimated standard deviation of the distribution of annual random effects; and $0.5\sigma_F^2$ is the lognormal bias correction factor.

2.3.6. Growth

Elements of size-transition matrix G_k , $G_{k,j^*,j}$, are annual size transition probabilities from size class j to size class j^* for sex k , which are calculated according to the framework of Sullivan (1992) as implemented in Zheng et al. (1995),

$$G_{k,j^*,j} = \int_{j_2^* - \partial}^{j_1^* - \partial} g(x|\alpha_{k,j}, \beta) dx, \quad (13)$$

where $g(x|\alpha_{k,j}, \beta)$ is a sex-specific gamma distribution with parameters $\alpha_{k,j}$ and β ; j_1^* and j_2^* are the lower and upper sizes of size class j^* ; and ∂ is the mid-point of size class j^* . When j and j^* are both the last size class, $G_{k,j^*,j} = 1$ as crabs do not molt to smaller size classes. Parameter $\alpha_{k,j}$ is a function of mean growth increment for size j , $I_{k,j}$, and β : $\alpha_{k,j} = I_{k,j}/\beta$. β was set to 0.75 (Zheng et al., 1998). Mean growth increment estimates were calculated from mean growth per molt estimates from Alunno-Bruscia and Sainte-Marie (1998) for females and from Somerton et al. (2013) for males:

$$I_{k,j} = f(l_{k,j}) - l_{k,j} \quad (14)$$

$$f(l_{k,j}) = \begin{cases} 1.16l_j + 4.475; & k=\text{female} \\ 1.17l_j + 6.593; & k=\text{male} \end{cases} \quad (15)$$

where $l_{k,j}$ is the mid-point of size class j .

2.3.7. Recruitment

Sex-specific annual recruitment to the immature population, $R_{k,y}$, was assumed lognormally distributed,

$$R_{k,y} = \bar{R}_k \exp(\sigma_{k,\delta} \delta_{k,y} - 0.5\sigma_{k,\delta}^2), \quad (16)$$

where \bar{R}_k is the mean recruitment; $\delta_{k,y}$ is an annual recruitment random effect with a standard normal distribution; $\sigma_{k,\delta}$ is the standard deviation of annual recruitment random effects and $0.5\sigma_{k,\delta}^2$ is a lognormal bias correction factor. The proportion of annual recruitment distributed to each size class, $d_{k,j}$, is calculated according to an estimated sex-specific lognormal density function evaluated at the mid-points of each size class, then constrained to sum to one:

$$d_{k,j} = \frac{f_k(j)}{\sum_j f_k(j)} \quad (17)$$

$$f_k(j) = (\sqrt{2\pi}l_j\sigma_k)^{-1} \exp((\ln(l_j) - \ln(u_k))^2 / 2\sigma_k^2), \quad (18)$$

where $\ln(u_k)$ and σ_k are the estimated mean and standard deviation of the lognormal density function and l_j is the mid-point of size class j .

2.3.8. Initial abundances and size distributions

Separate sex-specific abundances were estimated for each

population stage t at the start of the model time period: $N_{k,t,y=1982}$, where $t = i, n$ or o for females and $t = i$ or m for males. Size-specific proportions of $N_{k,t,y=1982}$ were distributed to each size class following an estimated lognormal distribution, as described by Eqs. (17) and (18) for recruitment size distributions. A separate lognormal distribution was estimated for each population stage of each sex: 3 distributions for females and 2 distributions for males.

2.3.9. Observation model and parameter estimation

Total predicted observed survey biomass for sex k , population stage t in year y , $\hat{B}_{k,t,y}$, is

$$\hat{B}_{k,t,y} = \sum_j N_{k,t,y,j} s_{k,j} w_{k,j}, \quad (19)$$

where $s_{k,j}$ are size-specific survey net selectivity values scaled by survey catchability values taken from the stock assessment report (Szuwalski and Turnock, 2016); and $w_{k,j}$ is the mean weight (kg) of individual crab for sex k and size class j . (Exploratory model runs that used selectivity and catchability values from Somerton et al. (2013) produced similar model results and estimates).

Measurement errors for biomass data were assumed lognormally distributed and for a given sex the biomass likelihood, L_B , is

$$L_B = 0.5 \left[\sum_t \sum_y (\log(\hat{B}_{k,t,y}) - \log(B_{k,t,y}))^2 / \sigma_{B_{k,t,y}}^2 \right], \quad (20)$$

where $B_{k,t,y}$ is the observed biomass for sex k and population stage t in year y ; \hat{B} is model estimated observed biomass; and $\sigma_{B_{k,t,y}}$ is the standard error of the log of observed survey biomass. Model size-specific annual catch estimates in numbers, $\hat{C}_{j,y}$, were converted to total annual estimated catch biomass, $\hat{C}_y^{bio} = \sum_j \hat{C}_{j,y} w_{k,j}$, and a lognormal likelihood evaluated annual catch estimates,

$$L_C = 0.5 \left[\sum_y (\ln(\hat{C}_y^{bio}) - \ln(C_y^{bio}))^2 / (\sigma_{C_y^{bio}}^2) \right], \quad (21)$$

where C_y^{bio} is the observed annual catch biomass and $\sigma_{C_y^{bio}}$ is the standard error of the log of the observed annual catch biomass. Size composition data is assumed to be sampled from a multinomial distribution; for a given sex the survey size composition likelihood is then

$$L_P = \sum_y n_e \sum_t \sum_j p_{k,t,y,j} \ln(\hat{p}_{k,t,y,j}), \quad (22)$$

where $p_{k,t,y,j}$ is the observed survey abundance proportion for sex k and size class j in population stage t in year y ; $\hat{p}_{k,t,y,j}$ is the predicted observed proportion and is calculated from $\hat{p}_{k,t,y,j} = s_{k,j} N_{k,t,y,j} / \sum_j s_{k,j} N_{k,t,y,j}$

where $N_{k,t,y,j}$ is the j^{th} element of abundance vector $\mathbf{N}_{k,t,y}$; $s_{k,j}$ is as defined in Eq. (19); and n_e is the assumed annual effective sample size of 200 (Szuwalski and Turnock, 2016). The fishery size composition likelihood is

$$L_F = \sum_y n_f \sum_j h_{m,y,j} \ln(\hat{h}_{m,y,j}), \quad (23)$$

where $\hat{h}_{m,y,j}$ is the estimated size proportion for a size class and year; h is the corresponding observed proportion; and n_f is the assumed annual effective sample size of 200 (Szuwalski and Turnock, 2016).

The sum of penalties common for both sexes: natural mortality and recruitment random effects and smoothness penalty for maturation probabilities is

$$Z_{0,k} = 0.5 \sum_y \delta_{k,y}^2 + 0.5 \sum_y \omega_{k,y}^2 + \sum_j \phi_{k,j}^2 \quad (24)$$

where $\delta_{k,y}$ is an annual recruitment random effect, $\omega_{k,y}$ is an annual natural mortality random effect; and $\phi_{k,j}$ is the value of the second differencing of the estimated size-specific maturation probability for

size class j . The final penalty value for male models ($k = \text{male}$) is $Z_k = Z_{0,k} + 0.5 \sum_y \omega_{F,y}^2$, where $\omega_{F,y}$ is the annual fishing mortality random effect. For female models ($k = \text{female}$), $Z_k = Z_{0,k}$.

The objective function to be optimized for a given sex is

$$O = L_B + L_P + L_C + Z, \quad (25)$$

where parameter values were estimated independently for each sex. The female model had 25 estimated fixed effects parameters: 6 for the initial size distributions, 3 for initial abundances, 10 for size-specific maturation probabilities, 2 for recruitment, 2 for the recruitment size distribution, and 2 for natural mortality. The male model had 39 estimated fixed effects parameters: 6 for the initial size distributions, 3 for initial abundances, 20 for size-specific maturation probabilities, 2 for recruitment, 2 for the recruitment size distribution, 2 for natural mortality, 2 for fishing mortality, and 2 for fishery selectivity. Parameter estimation was with maximum likelihood using the AD Model Builder (ADMB) software (Fournier et al., 2012), which optimized objective function O to estimate model parameters in a frequentist framework, using Laplace approximation to integrate out the random effects from the model likelihood (Maunder and Deriso, 2011). The annual random effects were estimated with Empirical Bayes methods, allowing them to be recorded and visualized (Maunder and Deriso, 2011). ADMB also estimates a parameter correlation matrix, which was examined for potential confounding between parameters.

3. Results

3.1. Female model

Estimated female survey biomass closely tracked observed survey biomass data across population stages with the fit to the observed survey data improving sequentially from immature to newshell mature to oldshell mature females (Table 1; Fig. 1A–C). The frequency of biomass estimates within the 95% confidence intervals (CI) of survey estimates were 29 in 36 years for immature females; 31 in 36 for newshell

mature females; and 35 in 36 for oldshell mature females (Fig. 1). The estimated mean annual survey size distributions (the mean of the 36 annual size frequency proportions for each size class with equal weighting for each year) for all three population stages were within the corresponding survey 95% confidence interval (Fig. 1C–E). Estimated mean natural mortality was 0.49 yr^{-1} (s.d. = 0.01) with a corresponding mean annual survival of 0.61 (s.d. = 0.01) (Table 1; Fig. 2A and B). Annual values varied from 0.04 yr^{-1} to 3.34 yr^{-1} . High annual values ($> 1.5 \text{ yr}^{-1}$) were estimated for 1984 (3.34 yr^{-1}) and 1993 (1.92 yr^{-1}); low annual values ($< 0.10 \text{ yr}^{-1}$) were estimated for 1986 (0.04 yr^{-1}), 1988 (0.08 yr^{-1}), and 2008 (0.09 yr^{-1}) (Fig. 2A).

Recruitment estimates showed episodic peaks at 1987, 2009, and 2016–2017 (Fig. 2C). Estimated maturation probabilities for the 30 mm and 35 mm size classes were zero and then increased monotonically to 1.0 with a sharp increase from the 45 to 55 mm size classes (Fig. 2D). No parameter correlations occurred between natural mortality, maturation, and recruitment estimates with $|r| > 0.7$. High correlations ($|r| > 0.7$) occurred between the means and variances of the initial population size distributions and between adjacent annual recruitment random effects.

3.2. Male model

Estimates of male survey biomass were very similar to observed survey biomass data (Fig. 3A and B); 32 of 36 annual immature biomass estimates and 33 of 36 annual mature biomass estimates were within the 95% survey CI. All model estimates of mean annual survey size distribution proportions (as defined for females) for immature and mature stages were within the corresponding survey 95% CI (Fig. 3C and D); both estimated and observed mean annual size distribution proportions had large 95% CI. Estimated mean annual natural mortality value was 0.36 yr^{-1} (s.d. = 0.07); annual values varied from 0.03 yr^{-1} to 0.91 yr^{-1} (Table 1; Fig. 4A). Low values ($< 0.10 \text{ yr}^{-1}$) were estimated for 1985, (0.04 yr^{-1}), 1986 (0.03 yr^{-1}), 2000 (0.06 yr^{-1}) and 2004 (0.08 yr^{-1}). Mean fishing mortality was 0.28 yr^{-1} (s.d. = 0.04) and annual estimates varied from 0.08 yr^{-1} to 0.52 yr^{-1} (Table 1;

Table 1

Estimated parameter values (except for maturation probabilities, see Figs. 2D and 4F). Imm, immature newshell; New, newshell mature; Old; oldshell mature; Mat, mature; All, all life-stages for a sex; RE, random effect.

Parameter category	Parameter	Symbol	Population stage	Female Value (C.V.)	Male Value (C.V.)
Initial size dist. (mm)	Mean	μ_k	Imm	46.8 (0.01)	55.3 (0.01)
			New	53.7 (0.01)	NA
			Old	55.8 (0.01)	NA
			Mat	NA	75.5 (0.01)
	S.D.	σ_k	Imm	0.2 (0.04)	0.3 (0.04)
			New	0.1 (0.04)	NA
			Old	0.1 (0.05)	NA
			Mat	NA	0.2 (0.05)
Initial abundance (10^7)		$N_{k,t,y}$	Imm	48.4 (0.05)	503.3 (0.14)
			New	319.0 (0.05)	NA
			Old	201.0 (0.06)	NA
			Mat	NA	129.5 (0.14)
Recruitment (10^7)	Mean	\bar{R}_k	Imm	176.8 (0.15)	258.8 (0.12)
	S.D. RE	$\sigma_{k,\delta}$	Imm	0.4 (0.12)	0.62 (0.13)
Recruit. size dist. (mm)	Mean	μ_k	Imm	42.1 (0)	38.4 (0.01)
	S.D.	σ_k	Imm	0.16 (0.01)	0.17 (0.06)
Natural Mortality	Mean	\bar{M}_k	All	0.49 (0.03)	0.36 (0.19)
	S.D. RE	$\sigma_{\omega,k}$	All	0.35 (< 0.01)	2.34 (0.16)
Fishing Mortality	Mean	\bar{F}	Mat	NA	0.28 (0.14)
	S.D. RE	$\sigma_{\bar{F}}$	Mat	NA	1.7 (0.07)
Catch size dist. (mm)	Slope	e_1	Mat	NA	0.33 (0.09)
	50% size	e_2	Mat	NA	102.0 (0.01)

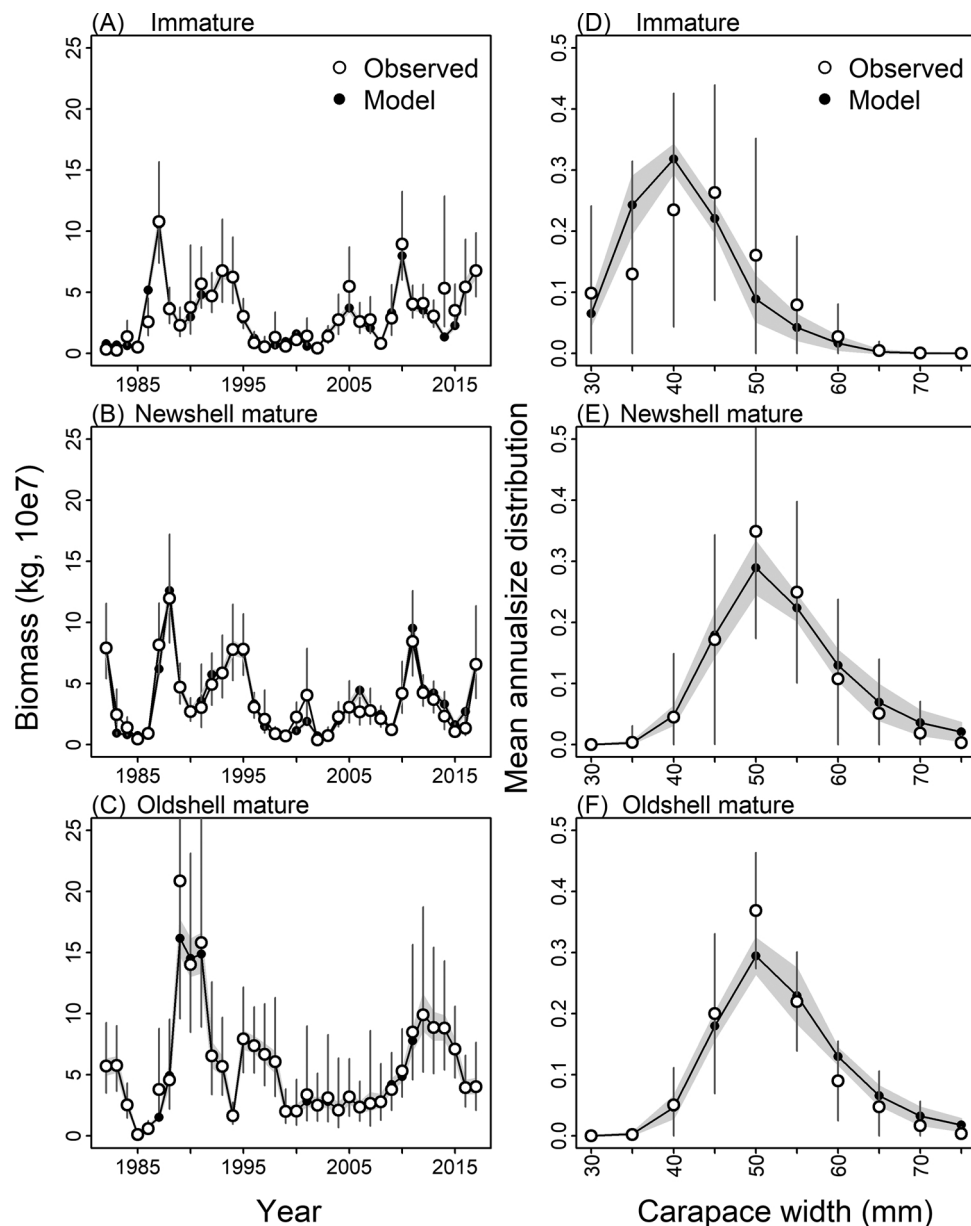


Fig. 1. Observed and model estimated survey biomass time series (left column) and mean annual survey size distributions (right column) for female snow crab, 1982–2017. Vertical lines: 95% CI for observed data; shading: 95% CI for model estimates. (95% CI for model biomass estimates difficult to observe; also, strong overlap between many observed and estimated values).

Fig. 4B). Generally lower fishing mortality values starting in 1999 coincided with imposition of stricter harvest quotas on the directed fishery (Fig. 4B). Predicted retained catch closely match observed retained catch (Fig. 4C); and predicted mean size frequency proportions of the retained catch also closely matched observed mean proportions (Fig. 4D).

Episodic recruitment peaks occurred in 1986, 1992–1993, and 2017 with low recruitment estimated from 1995 through 2014 (Fig. 4E). Maturation probabilities rose moderately between 50 mm and 90 mm size classes, and then sharply from the next four size classes (95–110 mm) to the asymptotic value of 1.0 (Fig. 4F). As with females, no parameter correlations between survival, maturation, and recruitment estimates occurred with $|r| > 0.7$. Persistent correlation patterns included strong negative correlations ($r < -0.7$) between the mean recruitment and most annual recruitment random effects and strong positive correlations ($r > 0.7$) between many recruitment annual random effects.

Additionally, an exploratory male model was also developed with the same shell condition based population stages and same population dynamics as the female model but with mature males subject to fishing mortality (results not shown). Model fits were good (e.g., similar to the female model for survey data) but a very high and seemingly unrealistic mean natural mortality (\bar{M}_k) of 1.07 (s.d. = 0.05) was estimated.

4. Discussion

A state-space model that utilizes shell condition data was shown to be a valid approach for both estimation of time-varying natural mortality for females and abundance estimation by maturity status and shell condition. The estimated mean female natural mortality is similar to other estimates for mature snow crab females: 0.56 yr^{-1} , Yamasaki et al., 2001; 0.56 yr^{-1} , Zheng, 2003; and 0.67 yr^{-1} , Drouineau et al., 2013. Murphy et al. (2017) estimated an M of 0.68 yr^{-1} for mature EBS females for the period 1980–2014 and 0.51 yr^{-1} for 1985–2014 using

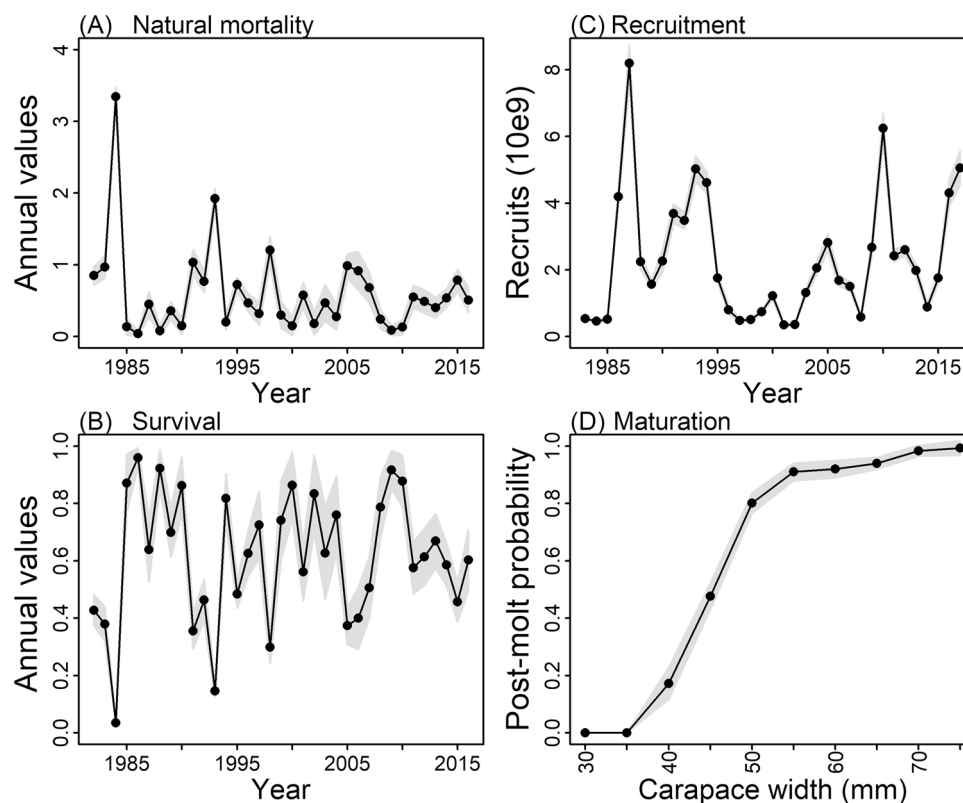


Fig. 2. Model estimates for female natural mortality (and corresponding annual survival), recruitment, and maturation probabilities. Shading: 95% CI for model estimates. (95% CI for some model estimates difficult to observe).

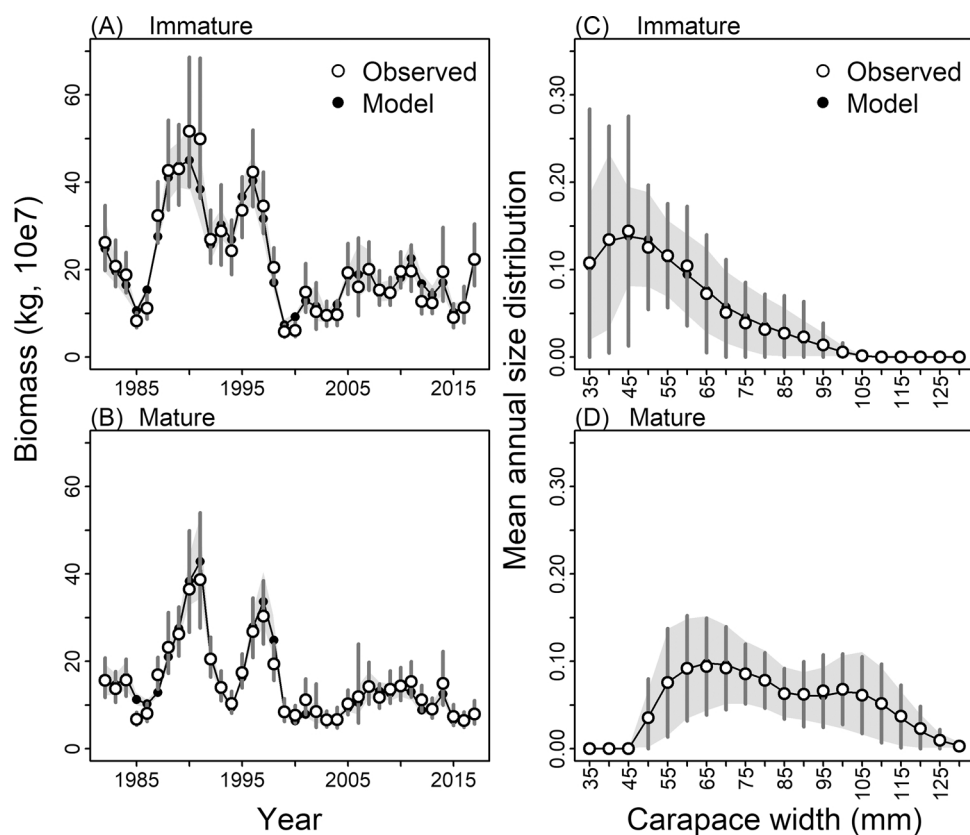


Fig. 3. Observed and model estimated survey biomass time series (left column) and mean annual survey size distributions (right column) for male snow crab, 1982–2017. Vertical lines: 95% CI for observed data; shading: 95% CI for model estimates. (95% CI for model biomass estimates difficult to observe; also, strong overlap between many observed and estimated values).

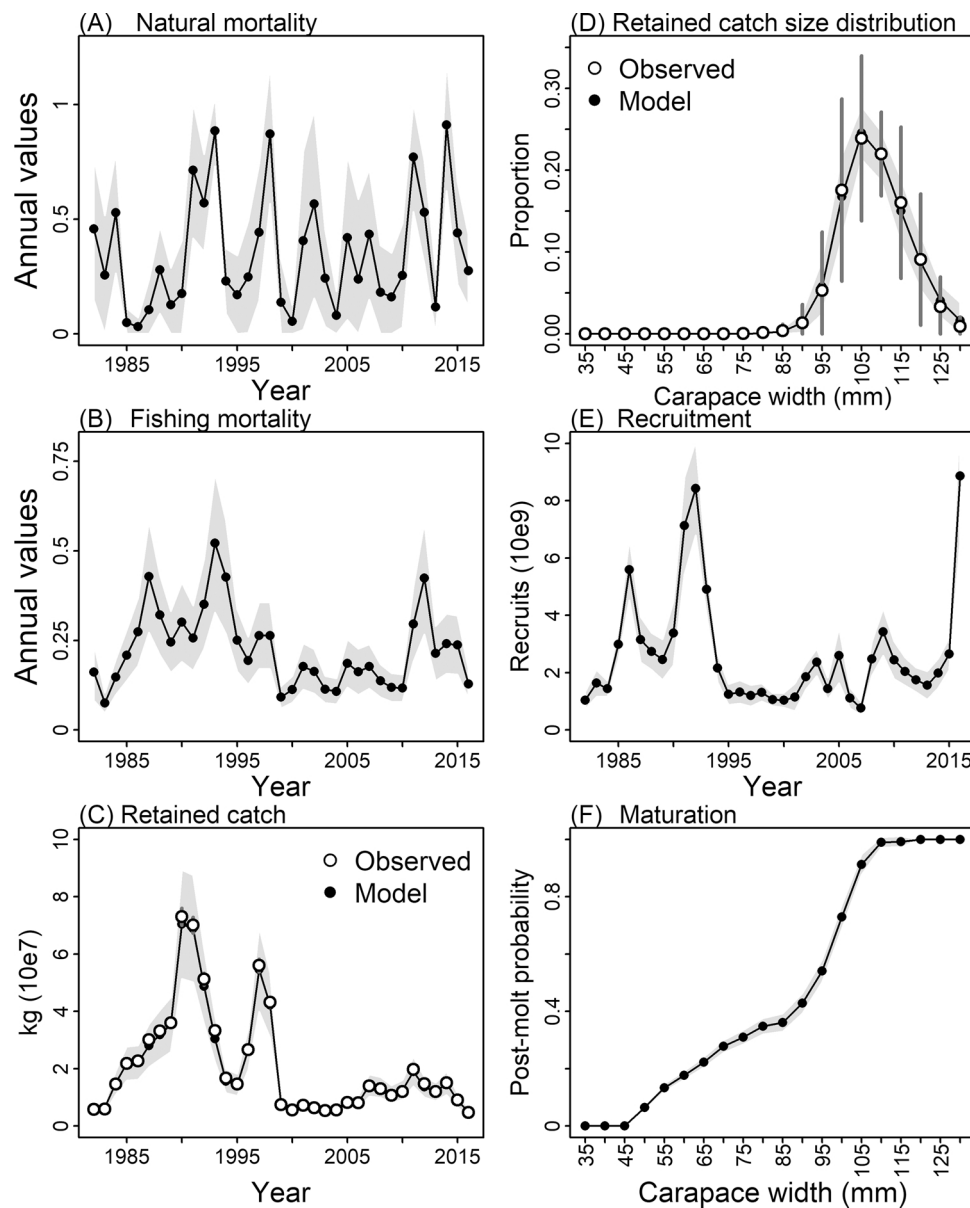


Fig. 4. Model estimates for natural mortality, fishing mortality, retained catch, mean annual retained catch size distribution, recruitment, and maturation probabilities. Vertical lines: 95% CI for observed data; shading: 95% CI for model estimates. (95% CI for some model estimates difficult to observe; also, strong overlap between many observed and estimated values).

the framework of [Drouineau et al. \(2013\)](#). These previous studies did not estimate annual values of natural mortality or include immature female dynamics. Of particular note is the estimate of 0.56 yr^{-1} by [Yamasaki et al. \(2001\)](#), which was based on tagging data and not on abundance estimates by shell condition like the other studies.

The episodic high and low annual values estimated for females indicate potential model overfitting. An autoregressive or random walk estimation framework ([Jiao et al., 2012](#)) may minimize or alleviate this issue. Additionally, estimation of separate immature and mature natural mortalities could be a further model refinement. The smaller size of immature females increases their vulnerability to groundfish predation relative to mature females ([Burgos et al., 2013](#)), while the energetic costs of egg production, physical injury from mating and mate-guarding by males ([Sainte-Marie et al., 2008](#)), and ontogenetic cross-shelf migration may incur a distinct suite of mortality-inducing factors on mature females.

Female model results rely on the assumption that shell misclassification for mature female snow crab is assumed negligible. While

[Ernst et al. \(2005\)](#) suggested female classification was straightforward for EBS females, this was based only on visual examination of crabs during the survey. [Drouineau et al. \(2013\)](#) provided more extensive confirmation with both field and laboratory data from the WNA. They described field classification of female shell condition as “easy” during spring and summer sampling and confirmed the accuracy of the classification with the age of stored sperm products within the spermathecae of a sample of collected females; sperm aging data was in 100% agreement with the field classification of shell class condition.

The successful modeling of female dynamics with the three life-history stages can be the first step to integrate estimation of annual and biennial spawner abundance into the EBS snow crab assessment model. Temperature-mediated spawning frequency has substantial impacts on EBS snow crab egg production and abundance estimates of annual and biennial female spawners is necessary for accurate egg production estimation ([Murphy et al., 2017](#)). While [Murphy et al. \(2017\)](#) estimated annual and biennial spawner abundances, their model only considered mature females and did not include immature dynamics (e.g.,

recruitment was to the newshell mature stage) or detailed size structure. Newshell females and oldshell mature females occupy different thermal habitats and are presumed to have different spawning frequencies (Rugolo et al., 2005; Murphy et al., 2011; Murphy et al., 2017). Integrating the modeling framework for annual and biennial spawning mature females of Murphy et al. (2017) and the female modeling framework here, a population model with immature dynamics and mature female stages further stratified into annual and biennial spawner stages can be developed.

The estimated mean natural mortality for males is in general agreement with longevity estimate of 7.7 years post-terminal molt for mature males from Fonseca et al. (2008). This 7.7 year estimate converts to a 0.39 yr^{-1} natural mortality when 5% of the original focal population is assumed alive at the maximum age (e.g., Cadigan et al., 2017) and to 0.55 yr^{-1} when 1.5% is assumed alive, as advocated by Hewitt and Hoenig (2005) for interpreting maximum age estimates. Cadigan et al. (2017) found an assumed value of natural mortality of 0.40 yr^{-1} produced the best fit for their model of WNA male snow crabs. While these estimates are based on mature male data, natural mortality between immature and mature males in the WNA is not thought to differ (Zheng et al., 2002). Annual male natural mortality estimates also had episodic high and low values and an autoregressive or random walk estimation framework for males may also be a useful model refinement as would potentially the separate estimation of immature male natural mortality. The possible influence of sampling variation on high and low natural mortality estimates for both sexes warrants further investigation.

While male shell condition data has low utility for population modeling, as evidenced by previous studies (Otto, 1998; Zheng, 2003) and from the results of the exploratory three stage male model described in this study, developing a male model with shell condition as done for females would be valuable for three reasons. First, the additional population structure would likely allow for time-varying estimation of immature natural mortality, based on other exploratory analyses performed. Second, the fishery targets clean, newshell-appearing males (NPFMC, 2000); thus, fishing mortality is more concentrated on a subset of younger mature males and its estimation could be further refined. Third, younger mature males captured by the fishery may not have participated in mating post-terminal molt before capture by the fishery (Sainte-Marie et al., 2008) and estimation of male abundances by shell condition may allow for further refinement of recruitment or reproduction related metrics such as sex ratio estimation.

Shell condition data aside, other informative data can be collected that would allow for accurate estimation of male newshell and oldshell abundances as done for females. Fonseca et al. (2008) show that measures of dactyl wear, counts of missing pereopods, and claw hardness are all correlated with post-terminal molt age. Individual values of these variables for a given crab, or a multivariate score may have valuable discriminatory capacities for EBS males. Additional radiometric aging data may also be valuable, even if such data is biased low as hypothesized by Fonseca et al. (2008). The sample size of available radiometric data for EBS mature males is too small to fully evaluate its effectiveness and, as it was collected in the mid-1990s, is fairly dated (Ernst et al., 2005).

5. Conclusion

Estimation of time-varying natural mortality for males and females, in addition to time-varying recruitment and fishing mortality, with a small number of parameters shows the value of a state-space modeling framework. While the model fits to the survey data are good, the plausibility of some of the natural mortality estimates needs further scrutiny. We consider the results to be preliminary and the models to be proof-of-concept approaches that have the potential, after further refinements and testing, to be either a complementary modeling framework to the current stock assessment model or considered as prototypes

for a next generation of EBS crab assessment models that use a state-space estimation framework. Further refinements to improve the model performance and mortality estimates include more detailed implementation of fishery bycatch dynamics; within model estimation of survey selectivities; implementation of an autoregressive or random walk framework for natural mortality estimation; and use of annual rather than time-averaged values of size-specific estimates of newshell proportion mature for estimation of mature male abundance and biomass.

While this study focused on variability in natural mortality, critical for understanding population dynamics and for population modeling (Jiao et al., 2012), the state-space approach may also allow for estimation of variability in other key biological processes such as growth and maturation (Otto, 1998; Orensanz et al., 2007; Zheng, 2008). This framework can also be readily applied to the congeneric EBS Tanner crab, which has a similar life-history, as well as to other snow crab and *Chionoecetes* populations in other regions.

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