



Full length article

Integrating demographic and environmental variables to calculate an egg production index for the Eastern Bering Sea snow crab (*Chionoecetes opilio*)James T. Murphy^{a,*}, Louis J. Rugolo^b, Benjamin J. Turnock^b^a Cascadia Sciences, 4403 Francis Ave. N. #4, Seattle, WA 98103, USA^b Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, 7600 Sand Point Way Northeast, Seattle, WA 98125, USA

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ABSTRACT

The complex life-history of the snow crab suggests that estimates of mature female biomass may not correlate proportionally with actual egg production. We calculate an egg production index (EPI) for the Eastern Bering Sea (EBS) snow crab using a simulation model that follows mature females from the molt-to-maturity through various reproductive stages (primiparous and multiparous) and reproductive cycles (annual and biennial). The model is parameterized with an estimate of annual instantaneous natural mortality, M , from a separate statistical model. The egg production model runs from 1980 to 2014, but the EPI is calculated only for 1985–2014 to be able to unambiguously assign mature females to the various component reproductive categories. Estimated M was 0.68yr^{-1} for 1980–2014. Linear regression of EPI lagged one year with stock assessment estimates of mature female biomass had an R^2 of 0.78, but with a mean absolute percent error of 82% between observed and model predictions; mature female biomass is thus a variable and uneven predictor of egg production. On average, primiparous females contributed 46% to total annual egg production and multiparous females the remaining 54%. Multiparous females in an annual cycle made the largest contribution to the EPI, responsible for 50% of annual egg production. Sensitivity analysis showed that egg production increased by a factor of 1.75 on average when only annual spawning was assumed. Multiparous females were found to co-occur almost exclusively with larger older males, such as those targeted by the fishery; due to the large proportion of egg production from multiparous females, this co-occurrence pattern has potential fishery management implications. The EPI will allow for future recruitment and population dynamics studies to use a more accurate measure of EBS snow crab reproductive potential, especially when considering the effects of climate change and environmental variability. Further demographic research will help refine EPI estimates.

1. Introduction

Egg production of a stock defines its reproductive potential (Lambert, 2008). Stock-recruitment analyses and other fisheries studies, though, typically use spawning stock biomass (SSB) as a proxy for egg production when quantifying reproductive potential (Marshall et al., 1998, 2006). Due to stock assessment or survey activities, estimates of SSB are typically more readily available than estimates of egg production, which require biomass or abundance estimates and estimates of fecundity and demographic structure, which are often lacking (Tomkiewicz et al., 2003; Lambert, 2008, 2013). Various studies have argued that SSB may be an imprecise proxy for egg production and reproductive potential (e.g., Trippel, 1999; Scott et al., 2006). A potential shortcoming of SSB as a proxy for egg production is the lack of consideration of the age structure of the female population (Cardinale and Arrhenius, 2000), which ignores possible maternal

effects (Shelton et al., 2012; Berkeley et al., 2004) such as egg quality and spawning duration (Scott et al., 2006), as well as failure to capture temporal and spatial demographic variability (Morgan and Rideout, 2008). Broad-scale patterns of egg production or other more demographically detailed indices of reproductive potential are not expected to differ substantially from broad-scale trends in SSB, but have the potential to provide for more nuanced analyses of recruitment trends and insights into the influence of environmental and fishing effects on a stock, especially if there is substantial demographic variability (Shelton et al., 2015; Morgan et al., 2011).

Due to the complex life-history of female snow crab (*Chionoecetes opilio*), SSB is a potentially problematic proxy for the reproductive potential of the snow crab stock in the Eastern Bering Sea (EBS), which supports an industrial-scale, male-only fishery. Mature female snow crabs have two reproductive stages that differ in per-capita fecundity (primiparous and multiparous stages, or less accurately, newshell and

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oldshell stages), can be in either an annual or biennial reproductive or spawning cycle, and may produce only partial clutches due to senescence or sperm limitation (Sainte-Marie, 1993; Rugolo et al., 2005). Accurate estimates of annual egg production necessitate accounting for these factors. Due to the lack of an estimation framework for egg production and the unknown relationship between mature female biomass and egg production, EBS snow crab is currently managed using mature male biomass to formulate overfishing definitions, evaluate stock status, and set harvest controls (NPFMC, 2008). Egg production estimates will allow the female component of the EBS stock to be incorporated into management reference points.

Studies in the EBS and the western North Atlantic (WNA) have shown that bottom water temperatures (water temperatures, hereafter) determine whether females express an annual or biennial reproductive cycle (Comeau et al., 1999; Moriyasu and Lanteigne, 1998; Rugolo et al., 2005). Mature females in an annual reproductive cycle hatch a clutch each year while those in a biennial cycle hatch one every two years. Based on *ex situ* experimental conditions, thermal exposure two to three months following egg extrusion is believed to determine whether a female expresses an annual or biennial spawning cycle (Webb et al., 2007). In WNA populations, biennial cycles occur where year-round temperatures are $< 1.0^{\circ}\text{C}$ or $< 0.75^{\circ}\text{C}$ (Kuhn and Choi, 2011; Sainte-Marie et al., 2008; Moriyasu and Lanteigne, 1998). Rugolo et al. (2005) found that female EBS snow crab inhabiting waters $< 1.0^{\circ}\text{C}$ also express a biennial reproductive cycle. Temperature could exert a profound influence on annual egg production for EBS snow crab because a large proportion of EBS mature female snow crab is typically below this biennial cycle threshold (Murphy et al., 2011).

The biennial spawning cycle has an especially strong influence on snow crab reproductive potential (Sainte-Marie, 1993; Comeau et al., 1999; Sainte-Marie et al., 2008). A crab on a strictly biennial cycle hatches at most half the number of clutches relative to a crab on a strictly annual cycle. In Bonne Bay (eastern Canada), mature females have an estimated longevity of five years and the discovery that these females were in biennial reproductive cycles reduced estimated expected number of lifetime clutches from 4 or 5 to a maximum of 2 (Comeau et al., 1999). Maximum longevity in the EBS for mature females has been estimated at 6 or 7 years (Ernst et al., 2005), and a strictly biennial cycle would lead to 3 versus 6 or 7 clutches for a female on an annual cycle. Additionally, the prevalence of biennial cycles correlates inversely with the size distribution of females, which also strongly influences egg production (Sainte-Marie et al., 2008). In colder waters, females mature at smaller carapace widths (Burneister and Sainte-Marie, 2010; Orensanz et al., 2007) and per capita egg production is strongly related to carapace width (Sainte-Marie, 1993).

Snow crab stock-recruit analyses have not employed estimates of egg production but rather have used stock assessment estimates of combined mature male and female biomass (Zheng and Kruse, 2003), or mature female biomass (Marcello et al., 2012; Szuwalski and Punt, 2013). Such approaches, while seemingly reasonable, ignore demographic factors such as biennial reproductive cycles that may result in estimates of total mature female biomass that have different temporal trends and magnitudes than those of actual egg production. Additionally, males and females have different growth rates and sizes and ages-at-maturity; therefore, male and female biomass trends can be out of phase, with mature biomass of one sex at a relatively high or low levels relative to the other sex (Sainte-Marie et al., 2008). Combined biomass estimates may conceal asynchronous biomass trends between the sexes and resulting highly skewed sex ratios (Sainte-Marie et al., 2008).

Armstrong et al. (2008) considered a suite of life-history and environmental factors in calculating an index of female reproductive potential. Their index, termed “female effective reproductive output” (FERO), scaled from 0.0–1.0 and closely tracked abundance indices developed within the same study. However, the lack of a population dynamics analytical framework that incorporates survival dynamics to explicitly link abundances of mature female categories across years

produced ambiguous and difficult-to-interpret estimates, resulting in the FERO index being currently unutilized in snow crab research and management deliberations.

In a given year and ignoring barren, nearly senescent crabs, the mature female snow crab population can be partitioned into six categories. Three categories are based on spawning cycle duration: crabs in an annual cycle, crabs in the first year of a biennial cycle, and crabs in the second year of a biennial cycle. Each of these categories can then be categorized by primiparous (females brooding their first clutch) or multiparous (females brooding their second or later clutch) reproductive stages (Moriyasu and Lanteigne, 1998; Comeau et al., 1999), which differ in egg production. Accurate estimation of annual snow crab egg production would need to account for these six components of the mature population. Determination of which females are in each reproductive cycle by reproductive state combination is not possible from available survey data. Until such data are available, realistic estimates of egg production require construction of a model capable of tracking these six components of the mature female population. Essential data inputs for such a modeling framework are annual estimates of abundances, size distributions, clutch fullness, proportions of mature females on annual versus biennial cycle, and annual survival.

EBS female snow crab experience a nominal amount of discard losses from the directed male-only fishery or bycatch from the ground-fish trawl fisheries (Turnock and Rugolo, 2014; Zheng, 2003); thus, annual female mortality is synonymous with natural mortality (Zheng, 2003). Mature snow crabs have ceased growth due to a terminal molt at maturation and estimation of natural mortality via a population model only has to account for changes in abundance due to recruitment to the mature component of the stock. Zheng (2003) developed such a statistical population model for mature female snow crab in the EBS to estimate annual instantaneous natural mortality (M , hereafter), partitioning the mature population into newshell and oldshell components. Drouineau et al. (2013) developed a similar statistical model to estimate mature female M in eastern Canada, but included annual mean carapace widths of newshell and oldshell females as an additional data input. To estimate M here, we implement the statistical framework of Drouineau et al. (2013), which also estimates annual mean carapace widths and survey abundances that will be used in the egg production model developed in this study.

A complementary analysis to estimating egg production is to describe and quantify which males are responsible for fertilizing the different categories of the mature female stock. Distinct spatial structure of both the EBS snow crab population and the snow crab male-only fishery has been long recognized and analyzed (Somerton, 1981; Otto, 1998; Zheng et al., 2001; Ernst et al., 2005). For this study a particularly important life-history process is the molt-to-maturity for females that occurs principally in the middle of the EBS shelf and is then followed by a migration to the deeper, warmer waters of the outer shelf (Fig. 1) (Zheng et al., 2001; Ernst et al., 2005). Several analyses have considered male and female distributions together. Using mapping analyses, Zheng et al. (2001) showed broad-scale distributions of males and females for various time periods. Murphy et al. (2011) described the more concentrated spatial distributions of females versus the more dispersed distributions of males. Based on thirty-three electronically tagged males, Nichol and Somerton (2015) examined the seasonal migration of large mature males relative to the summer distribution of mature female crab to identify mating associations of male and female EBS snow crab. As yet, quantitative analysis of the spatial and temporal trends in co-occurrence between males and females using survey data has not been performed.

The main objective of this study was to develop an egg production model that incorporates natural mortality, reproductive cycle duration, primiparous and multiparous stages, and clutch fullness dynamics to estimate relative annual egg production, which we term an egg production index (EPI); the EPI is assumed to be directly proportional to total egg production. Additionally, the model will quantify the

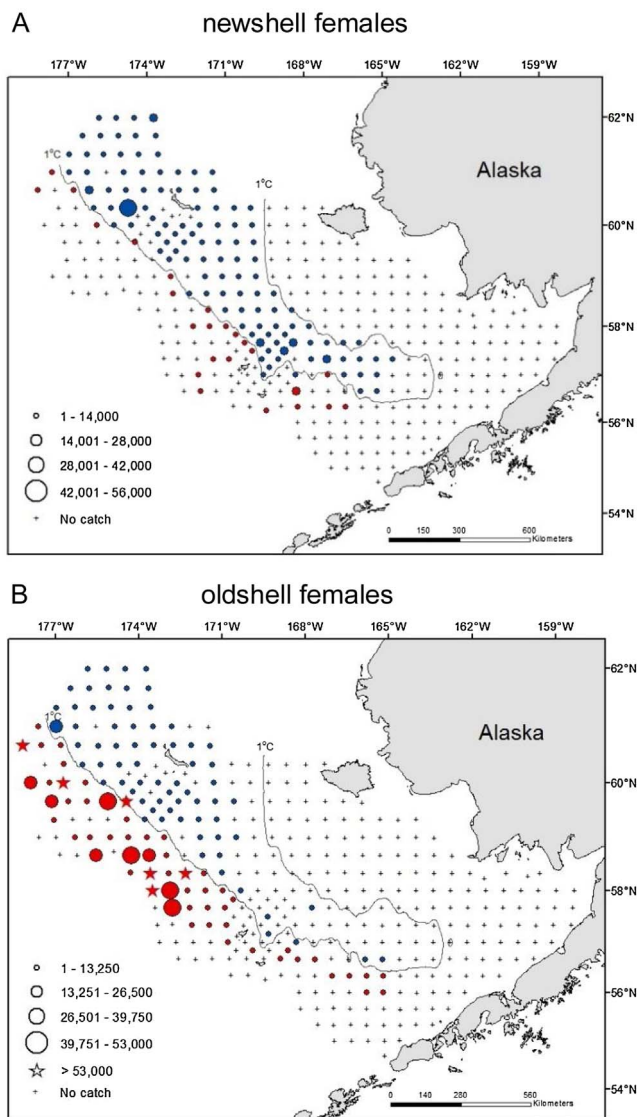


Fig. 1. Spatial survey abundances of mature female snow crabs in 2013. A: newshell females. B: oldshell females. Blue circles, abundances in areas with bottom water temperatures below 1 °C; red circles, abundances in areas with bottom water temperatures above 1 °C. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

contributions to egg production by the various components of the mature female population (primiparous/multiparous stages and annual/biennial reproductive cycles). We will assess the relationship between the EPI and stock assessment estimates of mature female biomass as well as assess the impact of biennial spawning on egg production. Finally, we also aim to quantify trends in spatial co-occurrence of males and females to link the egg production model results to the fisheries management framework.

2. Materials and methods

2.1. Relevant life history

Male and female snow crab undergo a terminal molt at maturity and cease growth thereafter. One biological data category collected on snow crab from the annual National Marine Fisheries Service (NMFS) bottom trawl survey is shell condition. Shell condition at the time of the survey is assigned based on several characterizations of shell pliability (whether soft or hard), dactyl sharpness, the amount of shell cleanliness, and the amount of epifaunal growth present. While there are

several levels of shell condition in this description, for the purpose of this study only two categories were used: new and old. Mature crabs classified as newshell are in their first year, post terminal molt, and these crabs move to the collective oldshell category in their second year after their molt to maturity as seen on the survey. Ovigerous crab that are newshell are termed primiparous (first-brood), while oldshell females brooding their second or later clutch are termed multiparous. Newshell mature females observed in the survey are assumed to have molted in the winter or spring of the survey year. Oldshell females observed in the survey are assumed to have molted-to-maturity at least one year prior. Primiparous females on a biennial cycle and one year past their molt-to-maturity would be classified as oldshell on the survey although their reproductive cycle and primiparous stage would be unknown. Non-ovigerous females can be either immature or barren mature, and can be distinguished on the survey by abdominal flap morphology. Primiparous and multiparous females have strong spatial differences in distribution due to ontogenetic migration, with primiparous females mostly occurring in shallower waters and multiparous females occurring in deeper waters.

2.2. Data

All data used in this study are from the annual NOAA Alaska Fisheries Science Center (AFSC) EBS bottom trawl survey, the principal resource survey for EBS crab and groundfish conducted annually since the 1970s (Daly et al., 2014), typically in June and July. Survey data on the distribution and abundance of crab and groundfish resources provides fishery-independent abundance estimates and biological data that support conservation and utilization decisions of the stocks. This study utilizes the NMFS survey data from 1980 to 2014. While earlier data are available, the survey covered much less area prior to 1980 and used different sampling methods. While sampling coverage and methodology did evolve after 1980, we believe the data collected from 1980 to 2014 are sufficiently coherent for this study. The survey is conducted using a static or lattice design on a 20 nmi x 20 nmi grid in depths from 20 m to 200 m. The current survey coverage, in place since 1987, samples approximately 376 stations, covering 140,350 nmi². Survey data provided by the AFSC listed data for only one haul per station. Relevant snow crab biological data collected include carapace width, sex, shell condition, egg color, and relative clutch size.

2.2.1. Biennial spawning temperature threshold

It is not possible to assign sampled mature female crabs to an annual or biennial cycle with existing survey data; thus, water temperatures at time of the survey are used as a proxy for the occurrence of biennial spawning for females who extruded eggs earlier in the year. Rugolo et al. (2005) found that females inhabiting waters at 1 °C or colder expressed a biennial spawning cycle while those in water warmer than 1 °C were in an annual cycle; thus, we use this temperature threshold to estimate the proportions of females by shell condition in annual and biennial cycles using water temperatures measured at the time of the survey. The reproductive cycle length appears determined by temperatures two to three months following clutch extrusion (Webb et al., 2007). Due to possible increasing water temperatures from time of clutch extrusion to the survey (Zhang et al., 2012), the extent of biennial spawning in the population based on survey data may be underestimated if the temperature threshold trigger occurs earlier than the survey. Here, the temperatures at the time of the survey are assumed indicative of reproductive cycle length for females with newly extruded clutches by being the maximum water temperature experienced by a female since clutch extrusion.

2.2.2. Clutch fullness

Clutch fullness values from the survey represent the fecundity of an individual female – specifically, the percent of eggs a female is brooding relative to the maximum clutch size based on carapace width.

Primiparous females have clutch sizes about 70%–80% of multiparous females of the same carapace width due to their eggs being developed in ovaries size-constrained by the pubescent (final pre-terminal molt development stage) body size prior to the molt-to-maturity (Sainte-Marie, 1993; Sainte-Marie et al., 2008); the molt-to-maturity allows for increased ovarian development resulting in larger clutch sizes. Partial clutches may occur due to incomplete fertilization from lack of sperm (Sainte-Marie, 1993) or senescence (Rugolo et al., 2005; Ernst et al., 2005).

The EPI model follows primiparous and multiparous females; and, ideally, clutch fullness values would be stratified by primiparous and multiparous stages. However, available data do not allow for such categorization. Newshell clutch fullness values from the survey represent the clutch fullness for newly mature primiparous females. Oldshell clutch fullness values are based on primiparous females one year into their biennial cycle in addition to all multiparous females. Given that oldshell values are based on a mixture of primiparous and multiparous females, oldshell clutch values are an approximation of true multiparous clutch fullness values.

Relative clutch fullness scores of 1, 2, 3, 4, 5, and 6 enumerated during the survey were converted to their representative proportions (0.00, 0.125, 0.25, 0.50, 0.75, and 1.00, respectively). Clutch fullness values of 6 represent a full clutch for a multiparous female and values of 5 represent a typical full clutch for a primiparous female (values of 6 for primiparous females are infrequent and represent extremely large clutches); lower values represent fractions of a full clutch and result from processes such as senescence or incomplete fertilization. Due to changes in field methodology and new clutch scoring criteria implemented after 1993 (Armstrong et al., 2008), values of 6 for primiparous (newshell) females for 1980–1993 were set to a value of 5 to standardize values across years.

2.3. Overview of analytical framework

The following population variables were estimated from survey data for 1980–2014 for each shell condition: mean temperature occupied, total abundance, abundance below 1 °C, proportion of total abundance below 1 °C, mean carapace width, and clutch fullness. Mean temperatures occupied are examined to assess broad-scale trends in occupied thermal habitat. Estimated abundances are relative indices of abundance for each category. Total abundance estimates and mean carapace widths are data inputs for the natural mortality model. Proportions of abundance below 1 °C and clutch fullness values are estimated inputs to the EPI model. The natural mortality model estimates M as well as abundances and mean carapace widths. The outputs of the natural mortality model are then used, along with the previously estimated population variables, to parameterize the EPI model. The EPI model calculates total relative egg production and relative production by the different components of the mature female population. The local index of collocation (LIC) is then calculated to estimate what male categories (based on carapace width and shell condition) co-occur with newshell and oldshell mature females.

2.4. Estimation of population variables

For estimation of snow crab population variables, the NMFS assigned survey stations into one of three contiguous strata (fewer in the early 1980s, reflecting changes in the geographical extent of the survey), with each stratum representing a specific geographic area. Estimation of population variables are then based on a stratified sampling design. All variables were estimated by shell condition for 1980–2014. Survey abundance estimates are unadjusted for survey catchability or gear selectivity and are thus relative indices. As noted in Zheng (2003), most mature females captured by the survey have carapace widths between 45 and 65 mm. Experimental trawling results indicate that gear selectivity for this size range is very similar

(Somerton et al., 2013), thus estimated mean annual carapace widths from the survey data are assumed to reflect actual population values.

2.4.1. Abundance and proportion of abundance below 1 °C

Point estimates and variances for total abundance and abundance occurring under 1 °C were based on area-swept stratified sampling methodology described in Kimura and Somerton (2006). Estimation of abundance occurring under 1 °C was similar to estimation of total abundance, with abundance at stations with temperatures ≥ 1 °C set to 0. Estimation of proportions of abundance below 1 °C also used a stratified sampling design and followed Manly and Navarro Alberto (2014) for estimation of proportions with stratified sampling.

2.4.2. Mean temperature occupied, mean carapace width, and mean clutch fullness

Stratum-specific weighted means were calculated based on mean values per station weighted by total abundance per station. Stratum-specific variances were based on the variance approximation for ratio estimators from Cochran (1977). Extrapolation to population-level point estimates and variances from stratum-specific values followed typical stratified sampling methodology as described in Kimura and Somerton (2006).

2.5. Natural mortality estimation

Data inputs to the natural mortality model are mean carapace width and survey abundance by shell condition and year (1980–2013 for newshell mature females and 1980–2014 for oldshell mature females). Estimated model outputs are a single value of M for the model baseline time period, annual survey abundances by shell condition, and annual mean carapace widths by shell condition. Newshell females transition to oldshell status after one year as assumed in Ernst et al. (2005) and Drouineau et al. (2013). The baseline model time period is 1980–2014, though shorter time period subsets are also examined.

2.5.1. Model description

Predicted abundance of oldshell females in year y , $\hat{N}_{O,y}$, is

$$\hat{N}_{O,y} = \hat{N}_{N,y-1}e^{-M} + \hat{N}_{O,y-1}e^{-M} \quad (1)$$

where \hat{N}_N is the abundance of newshell mature females, and M is the annual instantaneous natural mortality rate; \hat{N}_N and M are directly estimated parameters. Predicted mean carapace width for oldshell females in year y , $\hat{\mu}_{O,y}$, is

$$\hat{\mu}_{O,y} = \frac{\hat{N}_{N,y-1}\hat{\mu}_{N,y-1}e^{-M} + \hat{N}_{O,y-1}\hat{\mu}_{O,y-1}e^{-M}}{\hat{N}_{N,y-1}e^{-M} + \hat{N}_{O,y-1}e^{-M}} \quad (2)$$

where $\hat{\mu}_O$ is the mean carapace width of oldshell females and $\hat{\mu}_N$ is the estimated mean carapace width of newshell females; $\hat{\mu}_N$ is a directly estimated parameter. Abundance data measurement errors are assumed log-normally distributed and the negative log-likelihood for abundance, L_U , is

$$L_U = 0.5n \log \left[\frac{\sum_{y=y_s}^{y_e-1} (\log(\hat{N}_{N,y}) - \log(U_{N,y}))^2 / \log(\sigma_{U_{N,y}}^2) + \sum_{y=y_s}^{y_e} (\log(\hat{N}_{O,y}) - \log(U_{O,y}))^2 / \log(\sigma_{U_{O,y}}^2)}{\sum_{y=y_s}^{y_e-1} (\log(\hat{N}_{N,y}) - \log(U_{N,y}))^2 / \log(\sigma_{U_{N,y}}^2) + \sum_{y=y_s}^{y_e} (\log(\hat{N}_{O,y}) - \log(U_{O,y}))^2 / \log(\sigma_{U_{O,y}}^2)} \right] \quad (3)$$

where U_N and U_O are observed newshell/oldshell survey abundances; n is the total number of observed data points; y_s and y_e are the first year and last year of the model time period, respectively; and σ^2 terms are abundance variances.

Mean carapace width data measurement errors are assumed normally distributed and the negative log-likelihood for mean carapace width estimates, L_{CW} , is

$$L_{CW} = 0.5 \sum_{y=y_0}^{y_0-1} \left[\frac{\overline{CW}_{N,y} - \hat{\mu}_{N,y}}{\max(SE_{N,y}, 1)} \right]^2 + 0.5 \sum_{y=y_0}^{y_0} \left[\frac{\overline{CW}_{O,y} - \hat{\mu}_{O,y}}{\max(SE_{O,y}, 1)} \right]^2 \quad (4)$$

where \overline{CW}_N , \overline{CW}_O , SE_N , and SE_O are the observed survey mean carapace widths and standard errors for newshell and oldshell crabs in a given year. Standard errors < 1 mm are set to 1 mm, the minimum bin size for the data. Parameter estimates are derived by minimizing the overall negative log-likelihood, $L(\theta)$, where

$$L(\theta) = L_U(\theta) + L_{CW}(\theta). \quad (5)$$

For the baseline time period, 71 parameters were estimated: 1980–2013 newshell mean carapace widths (34 parameters, $\hat{\mu}_N$) and survey abundances (34 parameters, \hat{N}_N); oldshell abundance, \hat{N}_O (1 parameter), and mean carapace width, $\hat{\mu}_O$ (1 parameter), for 1980, the initial year of the model; and M (1 parameter). Estimation was performed with AD Model Builder software (Fournier et al., 2012), which provided point estimates and standard errors.

2.5.2. Catchability model

Implicitly assumed in the preceding model description is that survey catchability is constant. While little is known about temporal changes in survey catchability, survey gear changed in 1982 and geographic coverage changed in 1989; both factors may have affected catchability (Turnock and Rugolo, 2014). The EBS snow crab assessment model estimates survey catchability for female snow crab as a single value for mature females for three time periods: 0.89, pre-1982; 0.58, 1982–1988, and 0.55, post-1988 (Turnock and Rugolo, 2014). These estimates may be influenced by factors such as availability of crab to the survey, assessment model structure (e.g., growth, maturity and natural mortality), or other data components fitted in the model. To assess the possible influence of temporal changes in survey catchability as estimated from the assessment model, the natural mortality model was also run for the baseline time period using catchability estimates from the assessment. Here, values of \hat{N} for each shell condition and year in Eq. (3) were replaced by $q_y \hat{N}$, where q_y represents the year-specific catchability estimate from the assessment model.

2.5.3. Baseline and alternative time period models

The baseline model used data from 1980 to 2014. However, exploratory analyses revealed that different time periods of input data led to different estimates of M . To better understand temporal variability in M , the natural mortality model was run for a series of shorter time periods in addition to the baseline model. For these alternative models, the first year of the model time period varied sequentially from 1985 to 2010 by five year increments and each time period ended in 2014.

2.5.4. Estimation of M based on longevity

Longevity of mature females post molt-to-maturity has been estimated from 3 to 9 years in WNA and the EBS (Drouineau et al., 2013). To assess the validity of estimated values of M from the natural mortality model, natural mortality was calculated analytically based on values of assumed longevity post molt-to-maturity. Following the description in Nadon et al. (2015),

$$M_l = -\ln(S)/a_\lambda \quad (6)$$

where a_λ is assumed maximum age past molt-to-maturity, S is cohort survivorship to a_λ and is set at 0.05 (Nadon et al., 2015). M_l was calculated for $a_\lambda = 3, 4, \dots, 9$.

2.6. Egg production index (EPI) model

The EPI simulation model follows mature female abundances and their distribution across the six mature female categories through time. Fig. 2 gives an overview of how a cohort of newly mature females that

molted-to-maturity in year 0, is distributed across the six mature categories over subsequent years. The model calculates an annual EPI value, which is assumed to be directly proportional to total egg production. The EPI represents a relative index of annual egg production estimated using output from the natural mortality model, which is fit to relative survey abundances.

Data inputs to the model, estimated from the previous analyses, are: newshell mature female abundances, M , proportions of females occurring below the biennial reproductive cycle threshold temperature of 1 °C, and annual clutch fullness values. Model outputs include annual EPI values, mean annual percent of mature females releasing eggs, the mean annual percent of egg production by primiparous females (mean egg production by the multipara is the complement), and mean annual percent of egg production by reproductive cycle and stage: annual primiparous, biennial primiparous, annual multiparous, and biennial multiparous.

To completely enumerate the abundance of the mature female components through the baseline time period of 1980–2014 requires knowing the distribution of oldshell mature females among the six mature categories at the start of the model in 1980. While assumptions can be made regarding the composition of these oldshell females, we instead set the initial oldshell abundances in the first year of the model to 0 and identify the year where the percentage of total oldshell abundance comprised of newshell mature females followed since 1980 exceeds 95% of the oldshell population estimated from the natural mortality model; that is, the original oldshell females present in 1980 have died off, replaced by newshell cohorts from 1980 and later. The elapsed number of years will be a function of M and the abundance of oldshell females in 1980. From that year on, the assignment to the six spawning categories can be made for all mature females given model assumptions. The year that newshell mature females followed since the start of the model comprise at least 95% of oldshell abundance is termed the 95% threshold year. The EPI is then calculated from the threshold year to 2014.

2.6.1. Model description

The timing of life-history events has been simplified to minimize undue model complexity: molt-to-maturity, egg extrusion, and clutch hatching occur immediately prior to the survey. After egg extrusion, females enter either an annual or a biennial reproductive cycle and egg brooding lasts precisely one or two years. Newshell females are assumed to transition to oldshell status one year after molting to maturity. The model starts at year $y = 0$ denoting the year when the initial newshell cohort molts to maturity.

2.6.2. Primiparous abundances

$N_{N,y}$ denotes the abundance of a cohort of just molted-to-maturity, newshell, primiparous females in year y where values of $N_{N,y}$ are values $\hat{N}_{N,y}$ from the natural mortality model. The abundance of primiparous females one year past the molt-to-maturity in year y is the aggregate of individuals i) hatching eggs after an annual cycle, $N_{P,A}$; ii) completing the first year of a biennial cycle, $N_{P,B1}$; and iii) hatching eggs after completing a biennial cycle, $N_{P,B2}$, described by the following equations:

$$N_{P,A,y+1} = \left(1 - p_{N,y}\right) N_{N,y} e^{-M} \quad (7)$$

$$N_{P,B1,y+1} = \begin{cases} 0; & y = 0 \\ p_{N,y} N_{N,y} e^{-M}; & y > 0; \end{cases} \quad (8)$$

$$N_{P,B2,y+1} = \begin{cases} 0; & y \leq 1 \\ p_{N,y} N_{P,B1,y} e^{-M}; & y > 1; \end{cases} \quad (9)$$

where subscript P denotes primiparous status, subscripts A , $B1$, and $B2$ denote females that just completed an annual cycle, year 1 of a biennial

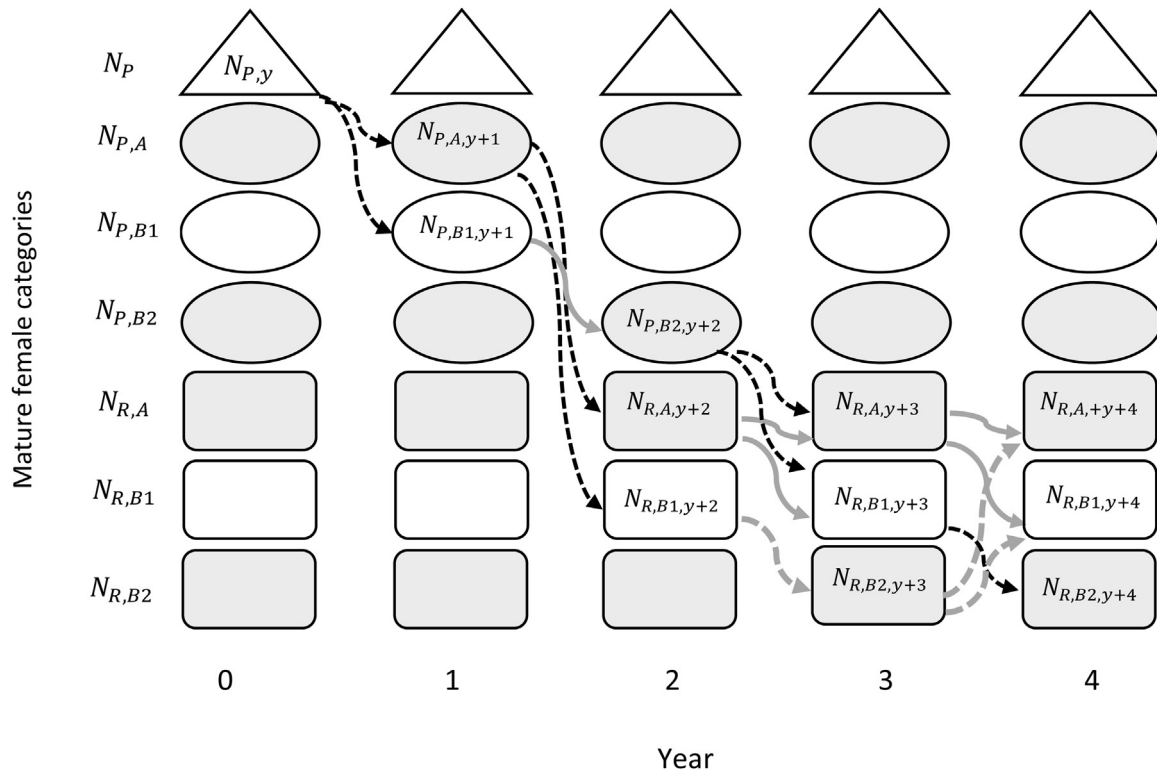


Fig. 2. Schematic of the temporal dynamics of a newshell mature cohort. All categories except N_p (triangles) are considered oldshell. Triangles: cohort of newshell primiparous females that molted-to-maturity in year y . Ovals: primiparous females at least one year past molt-to-maturity. Rectangles: multiparous females. Grey shade: females releasing eggs after specified reproductive cycle. Arrows denote one year of egg brooding for cycle at end point and survival of natural mortality (arrow formats only to aid viewing). Variable N , abundance. Subscripts: P , primiparous; R , multiparous; $A/B1/B2$ —females that completed annual cycle (A), first year of biennial cycle ($B1$); and second year of biennial cycle ($B2$).

cycle, and year 2 of a biennial cycle, respectively; and p_N is the proportion of N_N entering a biennial spawning cycle and its value is based on estimates from the survey data of the proportion of newshell females below the 1 °C biennial spawning threshold. After the hatching of the primiparous clutch, females enter an annual or biennial cycle as multiparous females.

2.6.3. Multiparous abundances

The abundances of multiparous females in year y is the aggregate of individuals i) hatching eggs after an annual cycle, $N_{R,A}$; ii) completing the first year of a biennial cycle, $N_{R,B1}$; and iii) hatching eggs after completing a biennial cycle, $N_{R,B2}$, described by the following equations:

$$N_{R,A,y+1} = \begin{cases} 0; & y \leq 1 \\ (1 - p_{O,y})(N_{P,A,y} + N_{P,B2,y} + N_{R,A,y} + N_{R,B2,y})e^{-M}; & y > 1; \end{cases} \quad (10)$$

$$N_{R,B1,y+1} = \begin{cases} 0; & y \leq 1 \\ p_{O,y}(N_{P,A,y} + N_{P,B2,y} + N_{R,A,y} + N_{R,B2,y})e^{-M}; & y > 1; \end{cases} \quad (11)$$

$$N_{R,B2,y+1} = \begin{cases} 0; & y \leq 2 \\ N_{R,B1,y}e^{-M}; & y > 2; \end{cases} \quad (12)$$

where subscript R denotes multiparous females and p_O is the proportion of multiparous females entering a biennial cycle.

The total female oldshell abundance in year y , $N_{O,y}$, is

$$N_{O,y} = N_{P,A,y} + N_{P,B1,y} + N_{P,B2,y} + N_{R,A,y} + N_{R,B1,y} + N_{R,B2,y}. \quad (13)$$

The 95% threshold year is the year when $N_{O,y}/\hat{N}_{O,y} \geq 0.95$, where $\hat{N}_{O,y}$ is the estimated oldshell abundance from the natural mortality model. For the threshold year and subsequent years, the abundance of each component of $N_{O,y}$ is slightly inflated by the scalar θ , such that

$\theta_y N_{O,y} = \hat{N}_{O,y}$. Without this minor adjustment, several more years are needed for $N_{O,y}$ to approximate $\hat{N}_{O,y}$ ($N_{O,y}/\hat{N}_{O,y} \geq 0.99$) and consequently several less years of annual EPI estimates are produced.

The number of eggs hatched by primiparous females year y , $E_{P,y}$, is

$$E_{P,y} = N_{P,A,y}f_{cw}(\hat{\mu}_{N,y-1})C_{N,y-1} + N_{P,B2,y}f_{cw}(\hat{\mu}_{N,y-2})C_{N,y-2} \quad (14)$$

$$f_{cw}(\hat{\mu}) = 10^{(2.616 \times \log_{10}(\hat{\mu}))} \quad (15)$$

where $\hat{\mu}_{N,y}$ is the mean carapace width of newshell females from the natural mortality estimation model; $f_{cw}(\hat{\mu})$ is the number of eggs produced by a multiparous female with carapace width $\hat{\mu}$, based on a relationship given in Sainte-Marie (1993); and C_N values are the mean clutch fullness values for newshell females after egg extrusion. Based on the relationship $f_{cw}(\hat{\mu})$, per capita fecundity increases roughly 5% per 1 mm increase in carapace width. The multiparous relationship between carapace width and fecundity is used for primiparous females because the clutch fullness values from the NMFS survey data adjust for the reduced fecundity of primiparous females. The number of eggs produced by multiparous females in year y , $E_{R,y}$, is calculated similarly with newshell abundances, carapace widths, and clutch fullness values replaced by oldshell values. The EPI in year y is then the combined values of the primiparous and multiparous EPI values,

$$EPI_y = E_{P,y} + E_{R,y}. \quad (16)$$

2.6.4. Comparison of EPI with mature female biomass estimates

The regression, $\widehat{EPI}_y = \alpha B_y$, is performed to quantify the relationship between EPI and stock assessment estimates of mature female biomass, a proxy for egg production similar to SSB for finfish stocks. Here, B_y is the stock assessment estimate of mature female biomass in year y from Turnock and Rugolo (2014), \widehat{EPI}_y is the predicted EPI value in year y , and α is the estimated slope of the regression. The purpose of

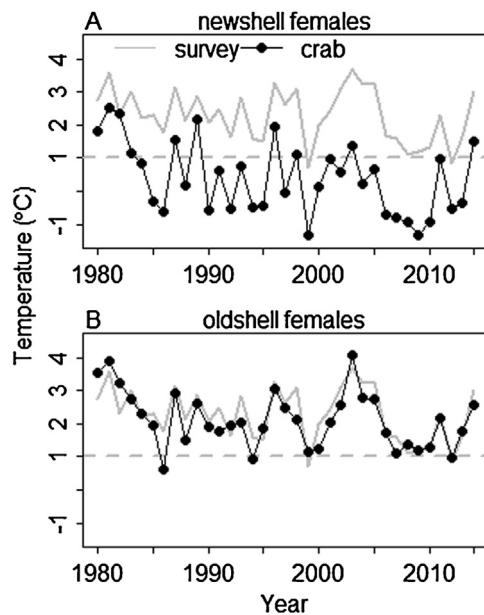


Fig. 3. Mean temperature occupied by mature females, 1980–2014, black line with filled circles. Grey solid line, mean survey temperature; grey horizontal dashed line, biennial spawning threshold (1 °C). A: newshell; B: oldshell.

the regression analysis is not to test hypotheses as in typical statistical inference, but to address how well mature female biomass predicts egg production – i.e., a predictive rather than an explanatory model *sensu* Shmueli (2010). Absolute percent error (APE) values are calculated to assess predictive power, where the APE for an individual prediction is $100[abs((\hat{EPI}_y - EPI_y)/EPI_y)]$. The mean APE (MAPE) and minimum and maximum values are reported.

2.6.5. Egg production by mature female categories

Besides an overall EPI, of interest are the fractional contributions from each reproductive category and their constituent spawning cycles to population fecundity. Primiparous EPI and multiparous EPI values along with the fractional contributions to total EPI by primiparous annual, primiparous biennial, multiparous annual, and multiparous biennial spawners are summarized.

2.6.6. Sensitivity analysis

The EPI model for the baseline time period of 1980–2014 is run under two different scenarios to assess sensitivity of the EPI to biennial spawning and clutch fullness values: i) only annual reproductive cycles (biennial cycle proportions $p_{N,Y}$ and $p_{O,Y}$ set to zero for all years); and ii) full clutches for all multiparous females ($C_O = 1$ for all years) with no changes to biennial proportions.

2.7. Spatial co-occurrence of adolescent and mature males with mature females

Survey data are analyzed to quantify the co-occurrence of males and females to identify mating associations. Survey data provide a snapshot of the summer spatial distributions though mating occurs mostly in late-winter and spring (Rugolo et al., 2005). Females are believed to undergo less extensive seasonal movements than males (Lovrich et al., 1995). Male movements from mating to the survey may distort observed spatial distributions in the survey data. However, analysis of tagging data of large (≥ 102 mm) adult males captured in the outer shelf indicated that, while some inshore movements occurred during the spring, adult males remained predominantly on the outer shelf throughout the year (Nichol and Somerton, 2015). Therefore, male-female spatial patterns observed in the survey data are consistent with

winter-spring mating assemblages.

The local index of collocation (LIC) (Wuillez et al., 2007) is calculated to measure of the degree of spatial co-occurrence between males and mature females. LIC measures the degree of co-occurrence among two different categories captured in a survey based on their proportional densities at individual sampling locations. LIC values of 1 indicate identical proportional distributions of both categories at all sampling locations; LIC values of 0 indicate the two categories did not occur at the same location. LIC is defined as

$$LIC = \frac{\sum_{i=1}^n z_{1,i} z_{2,i}}{\sqrt{\sum_{i=1}^n z_{1,i}^2 \sum_{i=1}^n z_{2,i}^2}} \quad (17)$$

where n represents the number of locations sampled, $z_{1,i}$ and $z_{2,i}$ are the densities of category 1 and category 2 at location i . We calculated LIC values for 1980–2014 between newshell and oldshell mature females and six male categories stratified by shell condition (new/old) and carapace width (small/intermediate/large): small, 50–79 mm carapace width; intermediate, 80–109 mm carapace width; large, greater or equal to 110 mm carapace width. Following the descriptions from Sainte-Marie et al. (2008), male maturity categories are described as either immature, adolescent (producing viable spermatophores, but not large-clawed, morphometrically mature), or adult (large-clawed, morphometrically mature males that underwent terminal molt). Based on shell condition, oldshell males are presumed to be almost exclusively adults with possibly a negligible number of skip-molters (non-adult, oldshell males) included, based on female skip-molting rates (Orensanz et al., 2007). The maturity status of newshell males is a mixture of immature, adolescent, and adult crabs with increasing percentages of adult males in the larger carapace width categories.

The distribution of station-specific abundances of mature females is typically highly right-skewed, due to a handful of stations representing relatively large proportions of total annual abundances. Exploratory analyses show that skewness in the female distribution combined with more uniform male distribution lowers the range of LIC values. Thus, while absolute LIC values are of interest, relative differences in LIC values among the various male-female combinations are the primary focus.

3. Results

3.1. Mean temperature occupied

The mean of newshell annual mean temperatures was 0.4 °C (s.d. = 1.1 °C) with a minimum mean temperature of −1.3 °C in 1999 and a maximum mean temperature of 2.5 °C in 1981 (Fig. 3). Newshell values were below the 1 °C biennial spawning threshold in 23 of the 34 years. A prolonged series of low mean temperature values occurred from 2006 to 2010 (range: −1.2 °C to −0.6 °C). The mean of oldshell mean temperatures was 2.1 °C (s.d. = 0.9 °C) with a minimum of 0.6 °C in 2000 and a maximum of 4.1 °C in 2003. Oldshell mean temperature values were below the 1 °C biennial spawning threshold in 3 of the 34 years. Correlations between occupied mean temperatures and mean survey temperatures were 0.80 for newshell females ($p < 0.001$) and 0.81 for oldshell females ($p < 0.001$). Newshell mean temperatures had a mean difference of −1.8 °C from the mean survey temperatures, while the mean difference for oldshell females was only −0.2 °C.

3.2. Abundance trends and proportions of abundance under 1 °C

For both shell conditions, abundance trends were cyclic with moderate to large peaks in the 1980s and 1990s, at lower levels in the 2000s, and showed an increase then decline from 2010 to 2014 due to a final recruitment pulse (Fig. 4A and C). For newshell females, mean

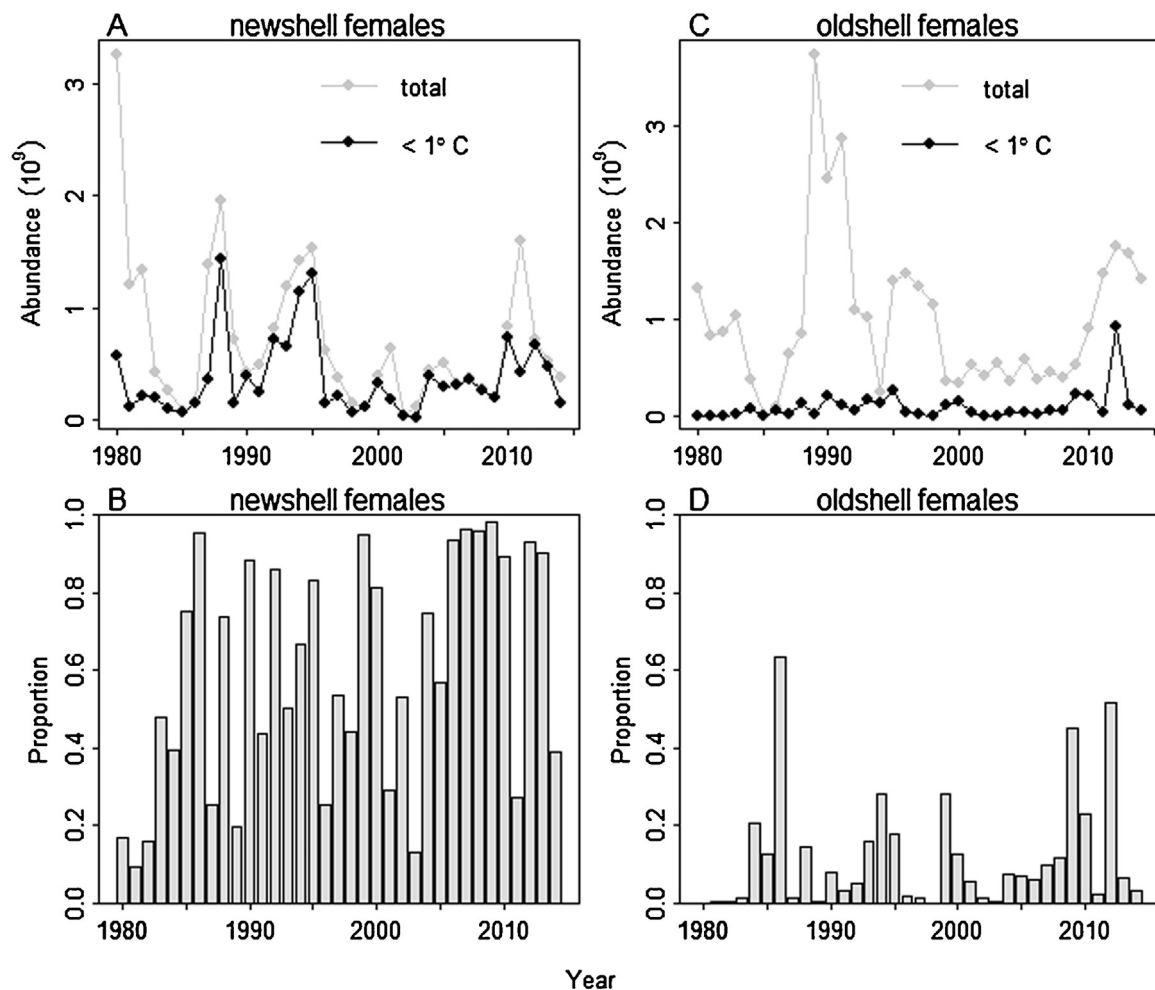


Fig. 4. Survey abundance data. A: Survey abundance of newshell mature females (grey line) and abundance of newshell mature females in waters below 1 °C biennial spawning threshold (black line), 1980–2014. B: annual proportions of newshell mature female abundance occurring under biennial spawning threshold, 1980–2014. C: same as A, for oldshell females. D: same as B, for oldshell females.

coefficient of variation (CV) values were 0.24 (s.d. = 0.07) for total abundance and 0.29 (s.d. = 0.09) for abundance under 1 °C. For oldshell females, mean CV values were 0.35 (s.d. = 0.12) for total abundance and 0.46 (s.d. = 0.15) for abundance under 1 °C.

Following from the results for mean temperatures occupied, newshell and oldshell females had sharply different trends of proportions of abundance occupying waters below 1 °C (Fig. 4B and D). Newshell females had consistently much higher proportions (mean = 0.60, s.d. = 0.30), with eight years greater than 0.90. Oldshell females had much lower proportions (mean = 0.12, s.d. = 0.15) with a maximum proportion value of 0.64 and with 21 years < 0.1. Correlations between mean survey temperatures and proportions under the biennial temperature threshold were -0.79 ($p < 0.001$) for newshell females and -0.64 ($p < 0.001$) for oldshell females.

3.3. Clutch fullness

The mean of clutch fullness values for newshell females for 1980–2014 was 0.74 (s.d. = 0.04), indicating that newshell mature females typically had full or very full clutches relative to their primiparous condition (Fig. 5). The mean of values for oldshell females was 0.78 (s.d. = 0.12) but these estimates were more variable than newshell values.

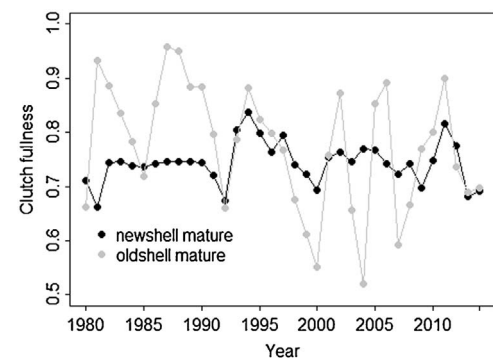


Fig. 5. Mean clutch fullness values for mature females by shell condition, 1980–2014..

3.4. Natural mortality model

For the 1980–2014 time period, estimated M was 0.68 yr^{-1} (s.d. = 0.06 yr^{-1} ; 52% survival fraction) for the baseline model (time-invariant survey catchability) and 0.66 yr^{-1} (s.d. = 0.06 yr^{-1} ; 51% survival fraction) for the time-variant catchability model. Given the similarity of these results, the simpler, baseline model was chosen for further analysis and use with the EPI model.

Estimated values of M varied by time period with a maximum value of 0.68 yr^{-1} for the baseline time period of 1980–2014, to a range of $0.40\text{--}0.43 \text{ yr}^{-1}$ for time periods after 2000 (Table 1). The decrease in

Table 1
Summary of results and model diagnostics from natural mortality model.

Model time period	No. estimated params.	M in yr^{-1} (s.d.)	% estimates within 95% survey CI			
			abundance		CW	
			new	old	new	old
1980–2014	71	0.68 (0.06)	82	57	94	100
1985–2014	61	0.51 (0.04)	86	60	97	100
1990–2014	51	0.56 (0.04)	92	60	96	100
1995–2014	41	0.50 (0.03)	100	60	95	100
2000–2014	31	0.43 (0.03)	100	73	93	100
2005–2014	21	0.40 (0.05)	100	70	100	100
2010–2014	11	0.41 (0.02)	100	100	100	100

estimated M from 0.68 yr^{-1} (1980–2014) to 0.51 yr^{-1} for 1985–2014 indicates that the early 1980s had strong influence on the estimation of M for the baseline time period. Estimates across time periods had good precision with a mean CV value of 0.08 (s.d. = 0.02).

The percentage of model point estimates of abundance and carapace width by shell condition that fell within the 95% confidence interval of

survey estimates were used as a model diagnostic (Table 1). Most model estimates of carapace width for all time periods and shell condition were within the 95% CI of survey estimates. For model estimates of abundance, the percent of estimates within the survey 95% CI increased as the model time periods shortened and newshell estimates had better fits to the survey data (higher percentages within the 95% CI) than oldshell estimates for all time periods. Model estimates of abundances and carapace widths followed survey abundance trends well (Fig. 6). CV values for model parameters were reasonable even though the model has many parameters. For the baseline model, mean CV values for estimated abundances were 0.44 for newshell and 0.26 for oldshell; mean CV values for carapace widths were 0.01 for newshell and 0.02 for oldshell.

Estimates of M_t based on assumed longevity for mature female snow crab post-maturity were 1.00 yr^{-1} , 0.75 yr^{-1} , 0.60 yr^{-1} , 0.50 yr^{-1} , 0.43 yr^{-1} , 0.37 yr^{-1} , and 0.33 yr^{-1} for $a_\lambda = 3, 4, \dots, 9$. Thus, the estimated M value of 0.68 yr^{-1} for the baseline time period translates to a longevity of about 4–5 years post molt-to-maturity, and the lowest estimated value of 0.40 yr^{-1} for 2005–2014 translates to a longevity of 7 years. The estimated M values from the natural mortality model fall within the range of values expected for mature female snow crab based on estimates of longevity post-maturity molt.

3.5. Egg production index (EPI) model

3.5.1. EPI and relationship to stock assessment biomass estimates

1985 was the threshold year when the abundance of newshell females from 1980 and later cohorts comprised a minimum of 95% of

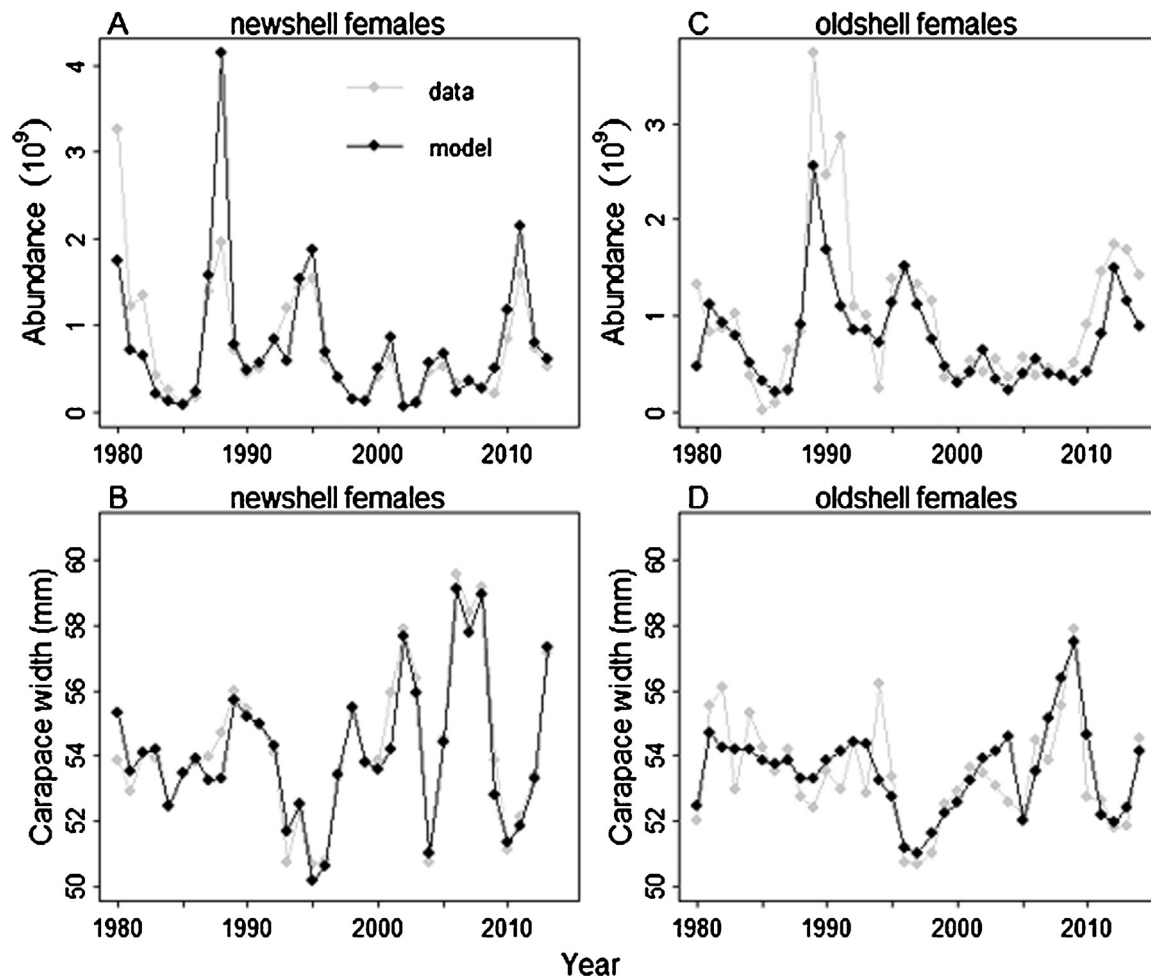


Fig. 6. Natural mortality model output. Observed data, grey; estimated model output, black. A: Newshell abundances, 1980–2013. B: Newshell mean carapace widths, 1980–2013. C: Oldshell abundances, 1980–2014. D: Oldshell mean carapace widths, 1980–2014.

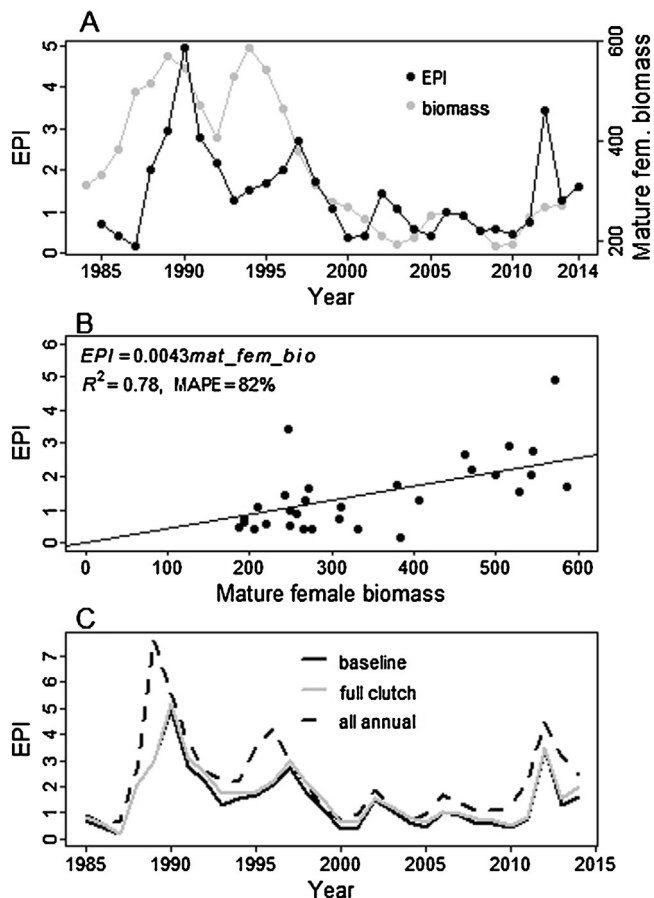


Fig. 7. EPI values (10^{13} eggs) from egg production model. A: EPI, 1985–2014; estimated mature female biomass (10^3 t) from stock assessment, 1984–2014. B: Regression line of EPI, 1985–2014, and mature female biomass (10^3 t), 1984–2013 (lagged one year). C: Sensitivity analysis: black: baseline EPI; solid grey: EPI with full multiparous clutches; dashed black: EPI with only annual reproductive cycles.

total oldshell abundance estimated from the natural mortality model; the EPI was then calculated for 1985–2014 (Fig. 7A). The EPI started at low values in 1985–1987 reflecting moderate to low abundances for that period with high rates of biennial spawning, rose sharply to a peak value in 1990, decreased sharply to an approximate plateau level in the mid-1990s, decreased to low levels through 2000s, and showed an increasing trend starting in 2010 with an episodic peak in 2012. The peak in 2012 is explained by a concurrent increase in estimated abundance for newshell females in 2011 (Fig. 6A) with a sharp decrease in newshell females entering a biennial cycle in 2011 (Fig. 4B).

The EPI for 1985–2014 was most strongly correlated (0.64, $p < 0.001$) with stock assessment estimates of mature female biomass lagged one year (1984–2013). At this lag, EPI followed the biomass trend but with large deviations, especially in the mid to late 1990s. The R^2 of 0.78 ($F = 106.2$, $p < 0.0001$) and a significant positive slope parameter ($p < 0.0001$) for EPI regressed on biomass (lagged one year) (Fig. 7B) indicates a linear relationship between egg production and mature female biomass; however, the high MAPE value of 82% with a maximum APE value of 895% indicates that while the EPI and female biomass are linearly related, mature female biomass is an uneven predictor of egg production, exhibiting a mixture of moderate to weak predictive capacities.

3.5.2. Egg production by mature female categories

On average, 37% of mature females in a given year release eggs (Table 2); this low percentage is due to the large proportion of mature abundance comprised of newly mature females which will not hatch eggs until the following year at the earliest, as well as by the proportion

of females one year into a biennial reproductive cycle. Except for multiparous females on a biennial cycle, the contributions to egg production by reproductive cycle and reproductive stage were considerably variable for 1985–2014 (Fig. 8), reflecting variability in abundances, rate of biennial spawning, mean sizes, and clutch fullness values. Primiparous females contributed, on average, 46% of annual egg production and therefore the multipara contribute the remaining 54%. Primiparous females on annual and biennial reproductive cycles contributed the same amount to annual egg production on average: 23% for annual cycles and 23% for biennial cycles. Multiparous females on an annual cycle contributed, on average, 50% to total egg production which was at least twice the value of the other categories. Multiparous females on a biennial cycle made minor contributions and were responsible for only 4% of egg production on average (Table 2).

Primiparous and multiparous EPI values (Fig. 8A) were strongly correlated with each other at a one year lag (0.78, $p < 0.0001$) with cyclic peaks in EPI values generally coinciding with peaks in abundances (Fig. 6A and C). A strong deviation from the correlation between EPI values occurs in 2012–2014, when a large, single-year peak in primiparous EPI in 2012 is not followed by a subsequent multiparous peak. This appears due to several factors: above average primiparous abundance in 2011 (Fig. 6A) relative to the preceding several years, relatively low proportion of primiparous entering a biennial spawning cycle in 2011 (Fig. 4B), and a relatively high proportion of multiparous females starting a biennial cycle in 2012 (Fig. 4D). Noticeably, the 2012 peak in primiparous abundance (Fig. 6A), which was higher than the 2011 value, actually resulted in much smaller EPI values in 2013 than the EPI values in 2012 due to the high proportion of primiparous spawners entering a biennial cycle that year. (Fig. 4B).

3.5.3. Influence of biennial spawning and clutch fullness values on EPI

For the baseline time period (with 95% threshold year = 1985) with only annual reproductive cycles assumed, the mean annual percent increase in egg production over the base model was 75% (Fig. 7C). When all multiparous females were assumed to brood full clutches, the mean annual percent increase in egg production was 19% relative to the base model.

3.6. Spatial co-occurrence of males and mature females

Large relative differences in LIC values exist between mature newshell and oldshell females and males (Fig. 9), indicating distinct patterns of spatial co-occurrence. Newshell females most strongly co-occurred with small newshell males (mean LIC = 0.53) followed by small oldshell males (mean LIC = 0.30), intermediate newshell males (mean LIC = 0.20), and intermediate oldshell males (mean LIC = 0.18). Little co-occurrence existed between newshell females and the large males of either shell condition (mean LIC values < 0.08). Conversely, oldshell females strongly co-occurred with oldshell males relative to newshell males. Mean LIC values for oldshell small, intermediate, and large males and oldshell mature females were 0.38, 0.51, and 0.29, respectively; mean LIC values for newshell males of all sizes and oldshell females were all ≤ 0.10 .

4. Discussion

The impacts of various demographic and reproductive factors such as biennial spawning, female size distributions, primiparous versus multiparous stages, and clutch fullness on snow crab egg production and population dynamics have long been recognized and considered for WNA stocks (Sainte-Marie et al., 2008, and references therein), and more recently for the EBS (Rugolo et al., 2005; Armstrong et al., 2008). This study, in particular, builds on the work of Armstrong et al. (2008) and Drouineau et al. (2013) to estimate the EPI by integrating the relevant factors in a population dynamics analytical framework. By

Table 2
Summary of results from EPI model.

Time period	95% threshold year	Mean% mature females releasing eggs (s.d.):	Mean total annual% egg production by category (s.d.)					Absolute percent error: mean (min,max)
			primiparous			multiparous		
			total	annual	biennial	annual	biennial	
1980–2014	1985	37 (22)	46 (22)	23 (22)	23 (15)	50 (23)	4 (6)	82 (5,895)

explicitly modeling abundances over time for the six categories of the mature female population and accounting for key demographic processes, detailed estimates of egg production were achieved. This population dynamics framework allows for straightforward sensitivity analyses with scenarios that changed the incidence of biennial spawning and clutch fullness values. Assuming all females were in an annual cycle led to a mean annual increase in egg production by a factor of 1.75, which is the same value estimated by Drouineau et al. (2013) for the same scenario. Other theoretical scenarios are possible, such as modeling egg production in a warming trend where a reduction in biennial spawning co-varies with an increase in mean female carapace widths given that female size at maturity is correlated with water temperature. (Orensanz et al., 2007; Sainte-Marie et al., 2008).

Two recent EBS snow crab recruitment studies used stock assessment estimates of mature female biomass as an explanatory variable in regression models with stock assessment estimates of recruitment, abundance of crabs 25–45 mm carapace width of both sexes (Marcelo

et al., 2012; Szuwalski and Punt, 2013). Neither study considered whether mature female biomass was a suitable proxy for reproductive potential. Marcelo et al. (2012) examined and discounted the importance of mature female biomass for EBS snow crab recruitment, while Szuwalski and Punt (2013) found mature female snow crab biomass an important explanatory variable for observed recruitment in the 1980s and 1990s, but not for later years. Complicating the evaluation of these conclusions is that both studies used time series of assessment model recruitment estimates which are now outdated due to changes in the snow crab stock assessment (J. Turnock, pers. comm.).

Whether use of the EPI in place of female biomass estimates would change conclusions of these studies regarding the role of the mature female stock to recruitment is not known. While snow crab recruitment may be independent of the stock component as these studies inferred, such conclusions may be premature without analyses that incorporate a more accurate representation of reproductive potential. However, both the EPI and mature female biomass show similar large-scale trends:

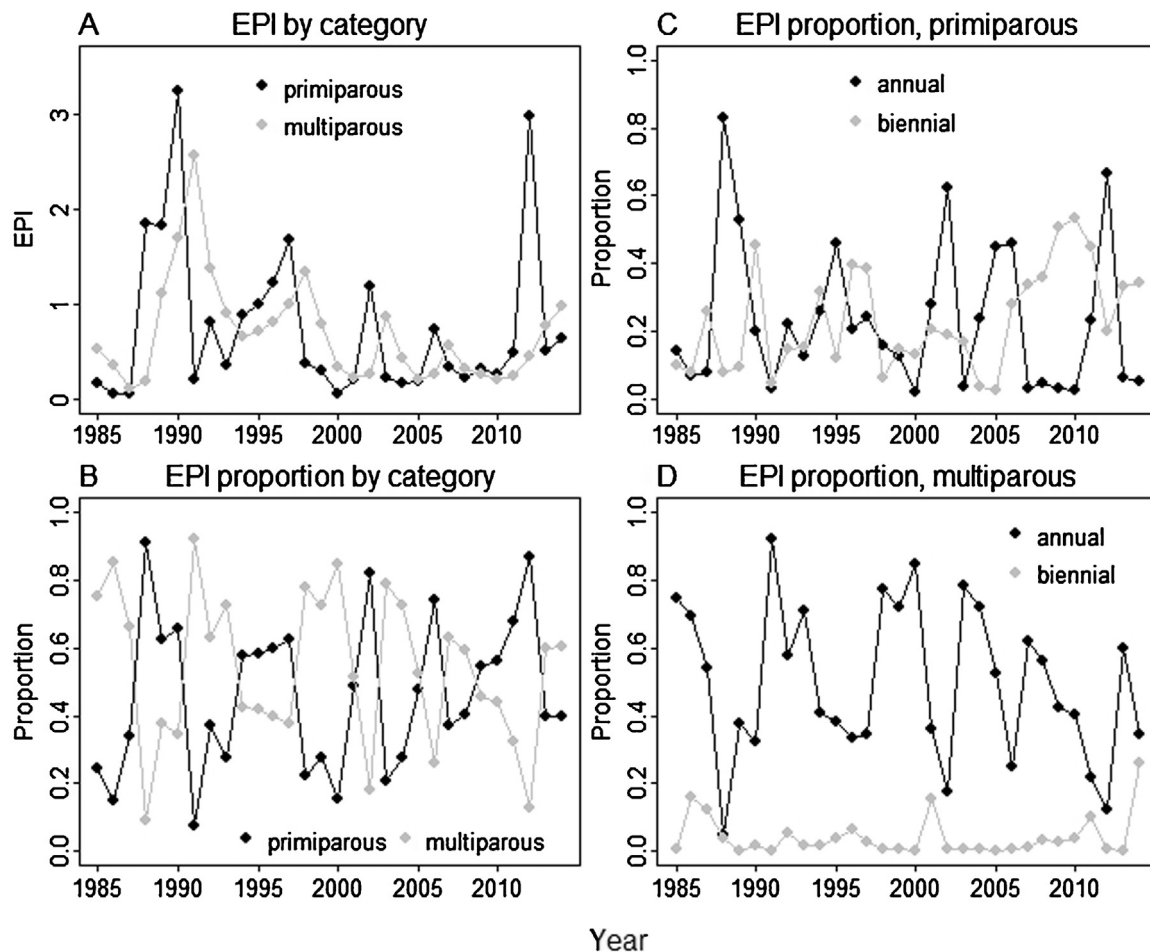


Fig. 8. Composition of egg production by mature female category, 1985–2014. A: EPI (10^{13} eggs) by primiparous and multiparous females. B: Proportion of total annual egg production from primiparous and multiparous females. C: Proportion of annual egg production from primiparous females in annual and biennial reproductive cycles. D: Proportion of egg production from multiparous females in annual and biennial cycles.

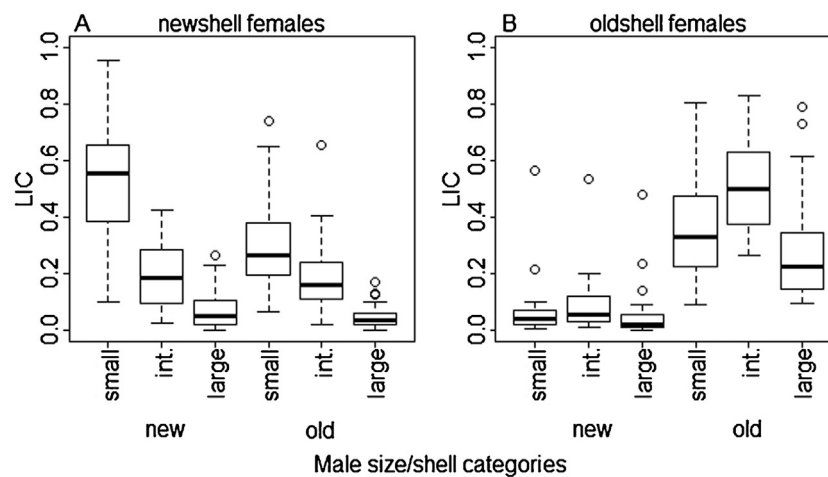


Fig. 9. Boxplots of annual local index of collocation values (LIC), 1980–2014; thick black lines median values. A: Annual LIC values for newshell mature females and six male categories by shell condition and size (newshell or oldshell; small, intermediate, large). B: LIC values for oldshell mature females and same six categories of males as for newshell mature females.

decreases after the 1990s and reduced levels through the 2000s with moderate increases in recent years. Elucidating the mechanisms behind this decline and lack of recruitment will not be answered by more accurate estimation of female reproductive potential alone, but will also require consideration of oceanographic variables, early life-history dynamics, trophic interactions, and possible fishery effects (Zheng and Kruse, 2006). While we consider the EPI the most accurate estimate of EBS snow crab reproductive potential to date, its ultimate utility will only be known if its use in recruitment studies and fisheries management metrics leads to different conclusions than use of proxies such as estimates of sex-specific mature biomass.

The EPI model results complement findings of Emond et al. (2015) and suggest a new framework for considering snow crab recruitment processes. Emond et al. (2015) found that abundances of newly settled benthic instars (age 0) in the northwest Gulf of St. Lawrence (eastern Canada) were both moderately correlated with larval production (egg production in this study) the year previous and moderately negatively correlated with sea surface temperature during the larval stage though only when larval production was low. Correlation of both larval production and age 0 abundance with age 2 abundance was weak, however; bottom temperatures were identified as the most important explanatory variable for predicting age 2 abundance (lower temperatures, higher abundances). Given that trends in recruitment can be modulated by both larval and early benthic survival, a reasonable inference is that conditions that maximize egg production and early benthic survival are important drivers of population regulation. For EBS snow crab, egg production is maximized both during periods of high mature abundance and when annual spawning is high. The EPI results for 2012 show that spikes in egg production occurred at moderate abundance levels and high levels of annual spawning for primiparous females. While admittedly speculative, a relative warm year (i.e., higher annual spawning) followed by a series of cold years (i.e., higher early-stage survival) may benefit snow crab recruitment, though density-dependent processes such as cannibalism (Emond et al., 2015) and climate-related current patterns (Parada et al., 2010) need to be considered.

For their study area in the Gulf of St. Lawrence, Drouineau et al. (2013) estimated the primiparous proportion of total annual egg production on average at 81% for 1991–2012, while this study of EBS snow crab estimates the primiparous proportion at 46% for 1985–2014. The Drouineau et al. (2013) estimate was made with the assumption that the entire mature female population operated on a biennial spawning cycle. Two reasons likely explain the difference between the studies: the generally overall lower rates of biennial spawning in the EBS and the lower rates of biennial spawning for multiparous females

relative to primiparous females. An overall lower rate of biennial spawning will shift egg production from the primipara to the multipara as this will increase abundances of multiparous females due to primiparous females only having to survive one year of natural mortality rather than two before joining the multiparous population. The lower rate of biennial spawning in multiparous females relative to primiparous females will further shift egg production to multiparous females as these females will hatch more clutches.

Similar to this study, Drouineau et al. (2013) reported substantial variability in annual proportions of total egg production contributed by primiparous and multiparous females, with varying primiparous abundance from periodic recruitment identified as the responsible mechanism. In the EBS, in addition to periodic recruitment of primiparous females, variability in annual-biennial spawning ratios and in clutch fullness of multiparous females drive variability in the relative contributions to egg production of primiparous and multiparous females. Further modeling is required to fully understand the scope of interactions between periodic recruitment of primiparous females, levels of biennial spawning, and clutch fullness in primiparous and multiparous contributions to total egg production.

We calculated that multiparous females contribute, on average, 54% of total egg production of EBS snow crab. Two studies described snow crab reproduction as either semelparous (Burgos et al., 2013) or quasi-semelparous (Emond et al., 2015), meaning that multiparous females make no or little contribution to recruitment. For the WNA, the description of quasi-semelparity may be apt as pervasive biennial spawning results in low multiparous egg production relative to the primipara (Drouineau et al., 2013). In contrast, EBS multiparous snow crab are predominantly annual spawners while primiparous females are predominantly in a biennial spawning cycle (Fig. 4). Burgos et al. (2013) based the hypothesis of semelparity on a simple correlation of newshell mature female survey abundances lagged six years with a proxy of newshell recruitment from Ernst et al. (2012). While a critical review of this analysis is infeasible here, we note that the results of Ernst et al. (2012) appear to be an artifact of employing the proportion of newshell abundance in the total mature female abundances as the index of primiparous recruitment rather than newshell abundances directly. Temporal variability in this proportion does not necessarily correspond to actual changes in newshell biomass. Further, repeating their analysis using oldshell abundances lagged with the same proxy of newshell recruitment also produced the same moderate correlation values (≈ 0.5), but these results were not presented in Ernst et al. (2012).

The granular detail of the EPI model provides critical insight into reproductive dynamics that further argues against the semelparity in

EBS snow crab. Most importantly, we found that primiparous and multiparous egg production to be strongly temporally correlated, and that multiparous egg production typically comprises at least one-half of total annual egg production. We consider it incorrect to attribute recruitment solely to primiparous females based on a time series of abundance data or similar proxies for stock and recruitment as in Ernst et al. (2012). These EPI results, as well as our inspection of the data in Ernst et al. (2012), suggest that multiparous and primiparous females are both significant contributors to EBS snow crab recruitment.

The results of the LIC analysis reveal that the relative contributions to total egg production between primiparous and multiparous females have potential fisheries management implications. In the EBS, newshell primiparous females co-occur predominantly with younger, smaller, and sexually mature male crabs below 102 mm carapace width, the minimum size accepted by commercial processors, thereby occurring outside the footprint of the fishery at the time of first mating. These younger, smaller males are therefore responsible for sperm provision for fertilization of the first-brood clutch of primiparous newshell females. As these females move ontogenetically to deeper depths of the outer shelf where multiparous mating occurs, they begin to co-occur with larger males within the footprint of the fishery. Sainte-Marie (1997) and Elner and Gass (1984) noted that ovigerous western Atlantic snow crab, particularly large females, can be less fecund in exploited than virgin stocks. Rugolo et al. (2005) found that female snow crab sampled in the area of the fishery showed diminished spermathecal reserves relative to females sampled in the northern EBS outside of the footprint of the fishery. The potential exists therefore for recruitment overfishing of this stock through disruption of fertilization of multiparous females. As the proportion of egg production from multiparous females increases (through decreased natural mortality or increased biennial spawning of primiparous females), the potential impact of the fishery on egg production and future recruitment would potentially increase.

The results of this study suggest the role that shell condition can play in snow crab population and assessment modeling. Using shell condition to categorize mature females, this study, Drouineau et al. (2013), and Zheng (2003), estimated similar values of natural mortality for mature females. Drouineau et al. (2013) used data where the classification of newshell and oldshell was routinely confirmed through examination of the color of stored spermathecal ejaculates in sampled females. Such data are not collected during the NMFS survey and leaves open the possibility of the results being influenced by shell condition misclassification. However, we believe that visual classification of snow crab into newshell and oldshell classes is similarly “easy” in the EBS as described by Drouineau et al. (2013). A variant of the natural mortality model can also be employed with mature males; given that males are subject to fishing, total mortality rather than survival from natural mortality could be estimated.

Estimated M values are similar to previously reported values for mature female snow crab of 0.66yr^{-1} from the WNA (Drouineau et al., 2013), 0.56yr^{-1} from the EBS for 1989–2002 (Zheng, 2003), and 0.56yr^{-1} from the Sea of Japan (Yamasaki et al., 2001). Estimation of mature female natural mortality was not the motivation of this study, but results from the natural mortality model show intriguing trends. Each time period analyzed in this model returned a different value of M , indicating that natural mortality is time variant, assuming that mature female survey catchability is similar for the time periods. While estimating annual, time-varying M was beyond of the scope of this study, it could be a useful refinement to the egg production model and contribute to the general understanding of snow crab dynamics. Female size-at-maturity is inversely correlated with abundance levels (Orensanz et al., 2007; Sainte-Marie et al., 2008); and the lower estimated M values are roughly correlated for time periods with lower female abundances. This suggests the possibility that size-at-maturity and natural mortality may both be density-dependent and co-varying processes. Mature females also occupied relatively high water tempera-

tures in the early 1980s, a period that influenced estimation of M ; temperature effects could be further examined. Annual estimates of M and possibly separate annual values for newshell and oldshell mature females will be necessary to understand overall variability in natural mortality, the roles of density-dependence and temperature, and possible co-variation between size-at-maturity and natural mortality.

The results of the natural mortality model rest on several assumptions. Critical assumptions are that newshell and oldshell crabs are correctly classified, survey catchability is the same for all mature female crab, no net immigration or emigration from the survey area, mature female mortality is a function of natural mortality only, and natural mortality is not size-dependent (Drouineau et al., 2013). Shell condition has been used extensively as a variable to study the spatial-temporal dynamics of EBS snow crab (Otto, 1998; Zheng et al., 2001; Zheng, 2003), and misclassification has not been previously identified as a source of error or concern. Drouineau et al. (2013) speculated that the behavior of oldshell females and/or their spatial distribution might result in lower catchability; however, no such issue has been identified for EBS females. Catchability may have changed due to changes in survey gear in 1982. However, incorporating time-specific catchability estimates for mature females from the assessment model resulted in a negligible change to the estimate of M . Whether females in the survey area function as a closed population is unknown, but the EBS snow crab population extends far north of the northern boundary of the survey area (Goddard et al., 2014). Possibly, spatially-stratified estimates of M , such as done in Zheng (2003) for northern and southern regions, could provide additional insights. Since almost all mature females are between the relatively narrow range of 45–65 mm, significant size-dependent natural mortality would not be expected.

Three sources of uncertainty in the EPI model results include the extent of biennial spawning, clutch fullness estimation for multiparous females, and the possible presence of unfertilized eggs in brooded clutches. Estimates of biennial spawning may be minimum estimates if significant warming of water temperatures occurred between egg extrusion and the survey. Utilizing data from physical oceanography models could possibly refine estimation of biennial spawning. Annual mean clutch fullness estimates for multiparous females were based on oldshell mature female fecundity data. As oldshell abundance estimates include oldshell, primiparous females one year into a biennial cycle, the multiparous estimates have some degree of bias. We believe the use of the oldshell fecundity relationship is the most reasonable approach to estimate clutch fullness for all categories of multiparous females, even though this includes oldshell primiparous females. Additionally, an implicit assumption for the EPI model is that all clutches have 100% fertilized eggs. However, EBS and WNA female snow crab have been observed to brood unfertilized eggs that eventually will be sloughed off (Rugolo, pers. comm.; Sainte-Marie and Carriere, 1995). The extent of brooding of unfertilized eggs in EBS snow crab clutches and the potential inflation of clutch fullness values is not known.

The results of our study depend on the various assumptions used to model survival and egg production. In addition to providing a more detailed and accurate estimate of snow crab reproductive potential, an additional value of the EPI is an impetus for continued and expanded demographic monitoring and research on the snow crab stock that will allow refinement of the EPI. Such research may generate data to further insights into snow crab reproductive biology, recruitment, and population dynamics in general, echoing a conclusion of Lambert (2013) regarding the utility of egg production estimates for the northern St. Lawrence Gulf cod (*Gadus morhua*). Additional field data on the prevalence of biennial spawning and clutch fullness by primiparous/multiparous categories would be especially valuable.

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