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Integrating demographic and environmental variables to calculate an egg production index for the Eastern Bering Sea snow crab (*Chionoecetes opilio*)

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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 °C or < 0.75 °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 °C also express a biennial reproductive cycle. Temperature could exert a profound influence on annual egg production for EBS now 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 (Burmeister 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 groundfish 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