

ARTICLE

Spatial and Temporal Variation in Annual versus Biennial Reproductive Cycles in Eastern Bering Sea Snow Crab *Chionoecetes opilio*

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Abstract

The stock assessment model currently used for the management of the fishery for snow crab *Chionoecetes opilio* in the eastern Bering Sea assumes an annual reproductive cycle. However, temperatures below 1°C can extend the snow crab reproductive cycle to 2 years, which could depress the total reproductive potential of the stock. Our objective was to determine the prevalence of snow crab in the eastern Bering Sea on a biennial reproductive cycle, relative to latitudinal and thermal gradients, and evaluate whether available bottom temperature data could be used to predict the proportions of biennial spawners. Mature female snow crab were collected on the annual National Marine Fisheries Service eastern Bering Sea bottom trawl survey during 2014–2018. Bimodality in the frequency distribution of oocyte area suggests that oocyte area can likely be used to distinguish annual and year-1 biennial spawners from year-2 spawners. In 2014, the highest rates of biennial reproduction were found in northern, colder areas in the eastern Bering Sea. In 2015–2018, very low rates of biennial reproduction coincided with warm temperatures across the eastern Bering Sea. This work could help in the estimation of female reproductive potential and allow the development of female-based reference points for the eastern Bering Sea snow crab fishery.

Reproductive output in crustaceans can be affected by a wide range of environmental variables, and although salinity and dissolved oxygen can have significant effects (reviewed in Green et al. 2014), temperature is the main driver for most species. Temperature can influence both age and size at maturity (Shields 1991), egg size and the

number of eggs per clutch (Hines et al. 2010), and embryo development rate (Green et al. 2014). Further, temperature is a key driver of female energetics, which can affect reproductive frequency. Two species of lobsters (American lobster *Homarus americanus* and European lobster *H. gammarus*) both exhibit a 2-year reproductive cycle in the

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colder part of their distribution, where they molt and mate in the summer of the first year, then extrude and brood their clutch over the second year; however, in warmer waters they are able to extrude immediately after mating and produce an additional clutch during the second year (Latrouite and Leglise 1981; Waddy and Aiken 1995; Agnalt and Kristiansen 2007). Similarly, in Alaska, Dungeness crab *Cancer magister* alternate between brooding a clutch one year and being barren for a second (Swiney et al. 2003), whereas in the warmer parts of their range they produce a clutch annually (Wild 1980). In both cases it is likely that lower energy availability and a slower metabolic rate in colder waters forces females to reduce the frequency of clutch production. Because female reproductive output has a substantial effect on the reproductive capacity of a population, differences in temperature among or within populations can have significant implications for the management of harvested crustacean species (Fischer and Thatje 2016).

The fishery for snow crab *Chionoecetes opilio* in the eastern Bering Sea is a male-only fishery, and management is informed by a stock assessment that uses annual mature male biomass as a proxy for reproductive potential, in part because the fishery is male only and in part because female reproductive output is difficult to quantify due to several factors, including biennial spawning (Szuwalski 2020). However, as embryos are produced and brooded by females, an understanding of female reproductive output is an important research priority for stock assessors and managers (Punt and Szuwalski 2014). Female snow crab have a temperature-mediated reproductive cycle, with warmer waters associated with annual cycles and colder with biennial cycles (Moriyasu and Lanteigne 1998). Following the terminal molt, females may produce clutches for 2 to 7 years (Bluhm and Shirley 2005; Ernst and Orensanz 2005), and a complete shift to biennial reproductive cycles could halve the total reproductive potential of the stock compared with solely annual reproduction (Webb et al. 2007; Sainte-Marie et al. 2008; Murphy and Rugolo 2017). Knowledge of the proportion of female snow crab across the eastern Bering Sea that are biennial spawners is needed to estimate the reproductive potential of the stock.

The timeline for snow crab reproduction varies between first-time spawners (primiparous crab) and females that have brooded at least one clutch (multiparous crab). Snow crab mate in winter to early spring, with primiparous females starting to mate in January and multiparous crab beginning in March and April (Ernst et al. 2005), although it is not necessary for multiparous crab to mate each year, given their ability to store sperm for use in fertilization of successive clutches (Adams and Paul 1983; Sainte-Marie and Carriere 1995). Extrusion of the clutch occurs soon after mating, typically from March to May, and the

temperature exposure early in embryogenesis, just following the extrusion of eggs, likely determines whether the reproductive cycle is annual or biennial (Webb et al. 2007). During an annual cycle, primiparous females have an incubation period of approximately 15 months and multiparous females of approximately 12 months (Sainte-Marie 1993; Moriyasu and Lanteigne 1998; Comeau et al. 1999) due to differences in the timing of egg extrusion and mating. For biennial spawners, multiparous and primiparous females extend this incubation period to approximately 24 and 27 months, respectively, giving snow crab one of the longer incubation periods of all invertebrates (Sainte-Marie 1993; Moriyasu and Lanteigne 1998).

The timing of ovarian and oocyte development also differs between annual and biennial spawners. In mature females, for both annual and biennial spawners, the mass of the ovaries and the gonadosomatic index (GSI) increases continuously after the extrusion of a clutch of eggs, but the process is slower in biennial spawners (Ito 1963; Sainte-Marie 1993). In a population with annually spawning snow crab, female GSIs have a unimodal distribution that increases linearly with time from extrusion (Ito 1963, 1967). The GSI of mature snow crab within annual populations is unimodal throughout the year, except right around the time hatching is occurring; at that point some snow crab have eyed eggs ready to hatch and fully mature ovaries (high GSIs) and others have newly extruded, uneyed eggs and empty ovaries (low GSIs; Ito 1963). In such populations, despite the difference in spawning times, primiparous and multiparous crabs cannot be distinguished based on their GSIs (Ito 1963). In a biennially spawning population, the GSI increases rapidly during the first year of oogenesis after the extrusion of a clutch and continues to increase, albeit less rapidly, during the second year (Sainte-Marie 1993). This produces a clear bimodal distribution in GSI throughout the year that likely distinguishes snow crab in their first and second year postextrusion (Kanno 1987; Sainte-Marie 1993). Similar to annually spawning populations, the GSI of primiparous and multiparous crabs are indistinguishable from each other (Sainte-Marie 1993). In Japan, snow crab oocytes start off at about 100–150 μm in diameter when they can first be distinguished and increase in size gradually over time until they reach 1.0–1.1 mm in diameter just before extrusion (Ito 1963; Kon and Honma 1970; Kon 1980). Because the increase in the size of the ovaries is primarily due to the increasing size of the oocytes, the GSI and oocyte size are tightly correlated, with the GSI increasing exponentially with oocyte diameter (Ito 1963).

Temperature appears to be the primary driver of embryonic development timing in snow crab. In the southern Gulf of St. Lawrence, eastern Atlantic snow crab become biennial spawners when water temperatures fall below 1°C (Moriyasu and Lanteigne 1998). Biennial

spawning occurs in the North Pacific Ocean (Rugolo et al. 2005; Kolts et al. 2015), but there are little data on the prevalence of biennial spawning or its link to temperature throughout the eastern Bering Sea. Modeling studies suggest that biennial reproduction can depress stock reproductive output, and management might be improved by the incorporation of egg production models and reference points that better represent complex female reproductive processes (Murphy et al. 2017).

Mature female snow crab in the eastern Bering Sea perform an ontogenetic migration from northeast to southwest (Zheng and Kruse 2001), resulting in differences in the distribution of primiparous and multiparous females in the eastern Bering Sea. Primiparous females typically dominate portions of the eastern Bering Sea shelf between the 50- and 100-m isobaths, while multiparous females are found farther out on the shelf beyond the 100-m isobaths (Zheng et al. 2001). As primiparous females age, they move from areas that are naturally colder year-round to deeper, warmer waters further south (Zheng et al. 2001). The spatial distribution for mature females suggests that primiparous females are more likely to exhibit a biennial cycle and multiparous females are more likely to exhibit an annual cycle, given that primiparous females occupy colder habitats.

Change to the reproductive tempo in snow crab, manifested as either an annual or biennial cycle, is likely attributed to bottom temperatures (Moriyasu and Lanteigne 1998; Webb et al. 2007), and changes to embryogenesis duration can directly alter key reproductive components for the stock, including interannual egg production and operational sex ratio. Not only does temperature influence physiological processes, such as gametogenesis and egg development, but also reproductive age (i.e., size at maturity; Orensanz and Ernst 2007). Consequently, year-class success is governed in large part by these temperature-driven processes, as shown for Tanner crab *Chionoecetes bairdi* (Rosenkranz and Tyler 2001). The coupling of temperature with reproduction and recruitment strength emphasizes the importance of clarifying potential effects on fecundity and stock reproductive output, with further study warranted for eastern Bering Sea snow crab. When snow crab are collected during the spring, shortly after annual spawners extrude eggs, embryos can be staged using a standard embryo staging timeline (Moriyasu and Lanteigne 1998) to differentiate annual and biennial spawners (Kolts et al. 2015). However, in the eastern Bering Sea, the most reliable sampling platform is the National Marine Fisheries Service (NMFS) annual bottom trawl survey, which samples snow crab from late June through August (Lang and Richar 2019). During these midsummer months, overlap in expected embryo stages between annual and biennial year-1 and biennial year-2 spawners makes embryo stage a less robust indicator of

reproductive cycle in wild populations. Additionally, variation in mating and extrusion time for primiparous and multiparous females leads to even greater overlap in embryo stages. Our specific objectives for this study were to (1) develop a method to distinguish year-2 biennial snow crab from annual and biennial year-1 snow crab captured in the bottom trawl survey, (2) estimate the prevalence of biennial snow crab along a latitudinal and thermal gradient, and (3) determine if measured bottom temperatures on the eastern Bering Sea survey can be used to predict the proportion of biennial spawning.

METHODS

Ovigerous snow crab were collected from June through August during the 2014–2018 eastern Bering Sea bottom trawl surveys. The survey covers an area of ~140,000 square nautical miles, divided into a 37-km × 37-km (20 nautical miles × 20 nautical miles) grid, and a bottom trawl sample is collected at the center of each; a total of 375 stations are sampled (Lang et al. 2019). All tows were conducted using a standard 83-112 eastern otter trawl employing an 83-ft headrope and a 112-ft footrope and followed NMFS bottom trawl standards (Stauffer 2004). With a pilot study in 2014, our goal was to assess our ability to discriminate between biennial year-2 and annual and biennial year-1 females and to determine if there were broad differences in the rate of biennial spawning across the population. Three sites consisting of 10 survey stations each were selected within the range of ovigerous snow crab in the northern, central, and southern regions of the eastern Bering Sea along a gradient of bottom temperatures. Within each site, three stations at which ovigerous snow crab were present were sampled. At each station, 30 ovigerous snow crab were randomly selected. In 2015–2018, we modified our sampling design and sampled across the entire population to calculate an overall biennial spawning rate and to test hypotheses concerning factors governing biennial reproduction. We randomly selected one out of every three stations at which 10 or more ovigerous snow crab were present and randomly selected up to 20 snow crab at each. Snow crab were preserved in 10% buffered formalin in seawater, with carapaces cracked open to speed preservation. Data from individual snow crab were paired to corresponding near-bottom temperature (NBT) and location data provided by the NMFS survey. The NBT for each station was calculated as the average of bottom temperatures collected while the net was determined to be on the bottom during the haul using a Sea-Bird SBE-39 data logger (Sea-Bird Electronics, Bellevue, Washington) attached to the headrope.

Snow crab carapace width (CW) was measured (to the nearest 0.1 mm), and shell condition (SC), a rough proxy for age since the last molt, was determined by external

examination of the carapace, legs, and dactyl tips for wear and the presence and size of epiphytic organisms (Lang et al. 2019). Samples included the following SC classifications: “2” for new, hard shell, “3” for old shell, and “4” indicating a very old shell (Jadamec and Donaldson 1999). Given that snow crab have a terminal molt to maturity (Conan and Comeau 1986), a clean shell without wear indicates a primiparous crab that extruded its first clutch earlier that year, while an older shell indicates either a multiparous crab or a primiparous crab in year 2 of a biennial cycle (Sainte-Marie and Sevigny 2002). This method is likely very accurate for mature female snow crab because they molt to maturity in a small time frame shortly before the survey and such clean-shelled snow crab are very easy to identify and differentiate from those with shells that are 12 months older; radiometric dating of carapaces supports the accuracy of this conclusion (Ernst et al. 2005). It is possible that SC3 snow crab may be erroneously categorized as SC2 if their carapace shows little sign of wear and epiphytic growth is minimal as may happen in cold, muddy habitats; however, the error rate, based on radiometric dating, is expected to be very low (Ernst et al. 2005). A subsample of embryos was removed from the center of each clutch to assess development according to the embryonic staging system characterized by Moriyasu and Lanteigne (1998) to determine if embryos were in an advanced, full stage of development (Kon 1980). Before staging, embryo subsamples were fixed in Bouin’s solution for 5 min, then rinsed with deionized water to increase the resolution of embryonic external morphology (Moriyasu and Lanteigne 1998). Ovary subsamples were randomly selected from the center of either ovary, extracted, and rinsed with filtered seawater. For each snow crab, 10 oocytes representative of the larger oocyte sample were imaged using Image Analysis software (Image Pro-Plus 7.0) at 50 \times magnification. Oocyte measurements have been proposed as a method by which to examine invertebrate reproduction given that oocyte size is independent of female size (Grant and Tyler 1983), and in measuring oocyte area, rather than diameter, we reduce potential bias associated with the imperfect sphericity of the oocyte. Oocyte area was calculated using Image Analysis software, after calibrating image size with a photo of a micrometer taken at the same magnification. Average oocyte area for each snow crab was used in subsequent analyses.

We hypothesized a priori that oocyte size would exhibit a bimodal frequency distribution because oocytes in biennial year-2 snow crab would be more developed and therefore larger than oocytes in annual and biennial year-1 snow crab; biennial year-2 snow crab would have extruded their current clutch of eggs more than a year prior to capture, allowing the current batch of oocytes a longer time to develop compared with the younger oocytes of annual and biennial year-1 snow crab. We expected this because a bimodal distribution in GSI distinguishes biennial year-1

from biennial year-2 snow crab (Sainte-Marie 1993), and the GSI is correlated with oocyte size (Ito 1963). Further, because the GSI of biennial snow crab increases more rapidly in the first year than in the second, both biennial year-1 snow crab and annual snow crab would have GSIs of about 22–25% of their maximum values 3 months after extrusion, indicating that the size of their oocytes would likely be indistinguishable from each other by size (Ito 1963; Sainte-Marie 1993). Although there may be a number of factors that influence oocyte size, including the energetic condition of individuals, the date of extrusion of the current clutch of eggs, and the local environmental conditions, for oocytes that had begun developing in the same mating or molting year, it would be expected that those factors would lead to variance in the data around a single mean rather than a bimodal distribution in oocyte size. We modeled oocyte area as a bimodal normal distribution, with two means (μ_1 and μ_2), two standard deviations (σ_1 and σ_2), and a mixing parameter (ω). The normal distribution with a smaller mean represents the annual and biennial year-1 cohorts, and the normal distribution with the larger mean represents the biennial year-2 cohort. The mixing parameter is the proportion of the population that is biennial year 2 (with the proportion of the population that is annual or biennial year 1 equal to $1 - \omega$). Eight females with embryos near or at hatching (stages 11–14) were excluded from all analyses as they had oocytes that were fully developed and ready for extrusion. Theoretically, we could have included this group in the data set and used a trimodal distribution, but there were too few of these snow crab to warrant this. In addition, three snow crab that exhibited visual characteristics of bitter crab syndrome (Taylor and Khan 1995) were excluded from analyses.

We fit the average oocyte size in 2014 to both the bimodal model and to a null unimodal model in R (version 3.4.3) using the *mle* (maximum likelihood) function in the *Stats4* package (R Core Development Team 2011) as per Bolker (2008), with parameters estimated using the quasi-Newton method. We calculated the Akaike information criterion adjusted for small sample size (AIC_c) and the AIC weights for each model and used them to select the best-fit model; models with a ΔAIC_c of less than 2 were considered to explain the data equally well (Burnham and Anderson 2002). To examine among-year differences in the rate of biennial spawning, we fit the data from all years to a null unimodal model and a series of similar bimodal models in which the μ_1 , μ_2 , and mixing parameters were modeled as linear functions of sampling years and selected the best-fit model as above.

The bimodal model proved to be the best-fit model for the 2014 data (see Results); therefore, we used these parameter estimates to calculate the oocyte size at which there was a 50% probability that an observation was part of either the larger or smaller modes. This probability was

used as a cutoff to classify snow crab as either an annual or biennial year-1 female (coded as 0 for the binomial models below) or a biennial year-2 female (coded as 1). To examine potential variables influencing the rate of biennial spawning, the data from 2014 were fit to a series of models in which the probability of a snow crab being classified as a biennial year-2 female (based on the cutoff above) was a function of a number of environmental or geographic (NBT, prior year NBT, latitude, location [northern, central, and southern eastern Bering Sea]) and biological (CW, SC) variables. Pearson's correlation coefficients were calculated among all continuous variables to identify the correlations among covariates. Only 2014 data were analyzed for this analysis because of the change in sampling design. Analogous analyses for subsequent years were not attempted because there were too few biennial snow crab sampled in 2015–2018 to quantitatively analyze the data (see Results). Shell condition was treated as a discrete variable with two levels: SC2 (snow crab newly molted to maturity) and SC3+ (snow crab that had molted to maturity at least 1 year prior); location was treated as a discrete variable with three levels: northern, central, and southern. Continuous variables (temperature, latitude, and CW) were modeled using a logistic equation as follows:

$$P_b = \frac{P_{\max}}{1 + \sum_i \left(\frac{V_i}{V_{50i}} \right)^{b_i}},$$

where P_b is the probability of a snow crab being biennial year 2, P_{\max} is the maximum probability of a snow crab being biennial, i is the number of continuous variables, V is the continuous variable (temperature, latitude, or CW), V_{50} is the value of the variable at which the P_b is 50% of the P_{\max} , and b is a slope parameter. If no continuous variables were included, then the denominator reduces to 1. In models that included a single discrete variable (SC or location), P_{\max} was allowed to vary linearly among all levels. In models where both SC and location were included, P_{\max} was allowed to vary linearly among all locations and SC was incorporated by multiplying P_{\max} by P_{SC2} for SC2 snow crab (this implicitly sets $P_{\text{SC3+}} = 1$ so that the P_{\max} is the P_{\max} for SC3+ snow crab at each location). Because latitude and location were (by design) nearly perfectly correlated with each other, we did not include both variables in any model. The data were fit to these models using maximum likelihood in R as above, assuming a binomial distribution of errors where $p = P_b$, and the best model was selected using AIC_c .

For years 2015–2018 when random sampling of ovigerous females occurred across the entire eastern Bering Sea snow crab range, population-level estimates of year-2 biennial spawners among SC3+ snow crab were

calculated. To account for differences in μ_1 observed in later years, we calculated separate 50% cutoffs for each year to distinguish year-2 biennial spawners, assuming μ_2 stayed the same but allowing μ_1 to vary. Abundance estimates of SC3+ snow crab were determined for each grid cell using CPUE estimates from the survey. The abundance estimates and the proportion of year-2 biennial SC3+ females by station were then used to compute the weighted average of year-2 SC3+ biennial snow crab for each year. There are two high-density sampling areas in the eastern Bering Sea survey, where samples are taken at the corners of the sampling grid cells as well as in the centers (Lang et al. 2019). For grid cells with associated corner samples, the abundance was calculated using the average CPUE of center and corner samples for that grid cell.

RESULTS

From 2014 to 2018, 2,240 ovigerous snow crab were processed for assessing annual and biennial spawning across the range of snow crab in the eastern Bering Sea. The size distribution of sampled snow crab across all years ranged from 36.5 to 90 mm with a mean \pm SD of 56.33 ± 8.26 mm (Supplement 1 in the online version of this article). In 2014, the bimodal model of oocyte sizes was unambiguously the best-fit model, with the unimodal model having a ΔAIC_c of 55.50. Average \pm SE oocyte size was 0.092 ± 0.002 mm² for individuals in the first mode, which we interpret as annual and biennial year-1 females, and 0.188 ± 0.036 mm² for individuals in the second mode, which we interpret as biennial year-2 females (Figure 1), with an estimated cutoff point of 0.158 mm² distinguishing the two modes. Throughout this paper we will refer to animals in the first mode as annual and biennial year-1 snow crab and those in the second as biennial snow crab; however, we acknowledge that this is an interpretation of the data, that we do not know the reproductive state of the animals, and that it is possible other factors might be causing this bimodal distribution. Average \pm SD oocyte size for the eight females with embryos close to hatching was 0.314 ± 0.056 mm².

When fitting the oocyte data from all years (2014–2018), we were initially unable to get a good estimate of μ_2 , corresponding to biennial year-2 oocytes (the model fit estimated μ_1 and μ_2 values of 0.071 and 0.114 mm², respectively, which are both clearly in the lower mode of the oocyte size distribution in 2014; Figure 1). Fewer than 3% of snow crab sampled across all years were biennial year-2 snow crab when using the cutoff from the 2014 analysis. We therefore included models in which μ_2 and σ_2 were fixed to the estimates obtained from the 2014 analysis. In the best-fit model, μ_1 and ω varied among years (Table 1). It was visually apparent that the μ_1 and ω values

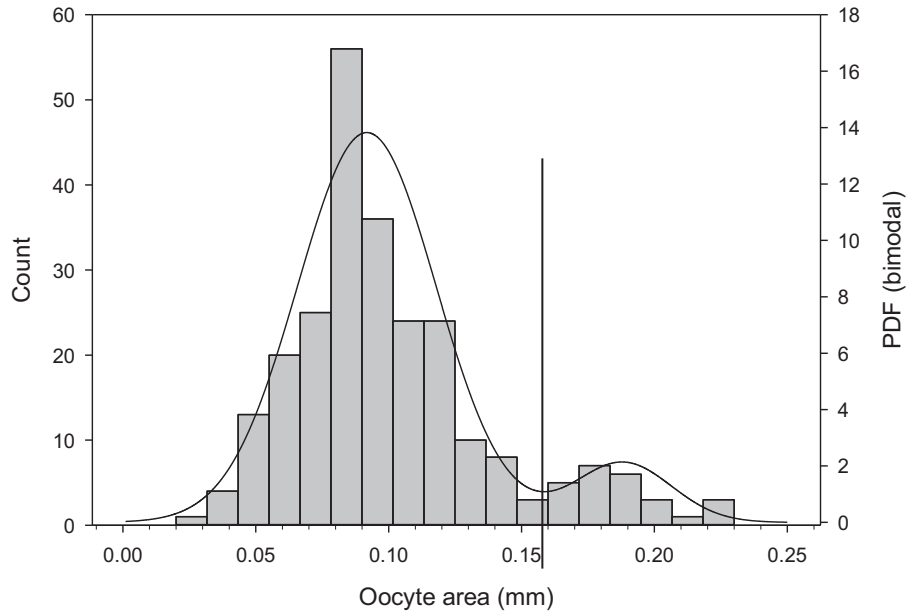


FIGURE 1. Oocyte area frequency distribution for eastern Bering Sea snow crab females in 2014. The black curve shows the probability density function (PDF) for the bimodal model fit to the oocyte area frequency distribution. The solid vertical line displays the 50% cutoff for biennial spawners (0.158 mm²).

TABLE 1. Akaike information criterion (AIC_c) values of models of oocyte size in eastern Bering Sea snow crab ovaries in 2014–2018. For the models, (Y) indicates that a parameter was treated as a linear function of year; (‘14,r) indicates that a parameter was a linear function of year, with 2014 differing from the rest of the years; and (f) indicates that the parameter was fixed to a value estimated using the 2014 data (see text for explanation). The column heading K indicates the number of parameters in each model.

Model	K	AIC _c	ΔAIC _c	Likelihood	AIC _c weight
$\mu_1 (Y), \sigma_1, \mu_2 (f), \sigma_2 (f), \omega(Y)$	10	-9,395.41	0.00	1.00	0.76
$\mu_1 (Y), \sigma_1, \mu_2 (f), \sigma_2 (f), \omega(‘14,r)$	13	-9,393.14	2.27	0.32	0.24
$\mu_1 (‘14,r), \sigma_1, \mu_2(f), \sigma_2 (f), \omega(‘14,r)$	8	-9,380.58	14.83	0.00	0.00
$\mu_1, \sigma_1, \mu_2, \sigma_2, \omega$ (bimodal)	5	-9,370.47	24.94	0.00	0.00
$\mu_1 (Y), \sigma_1, \mu_2 (f), \sigma_2 (f), \omega$	9	-9,368.56	26.85	0.00	0.00
$\mu_1, \sigma_1, \mu_2 (f), \sigma_2 (f), \omega$	5	-9,277.34	118.07	0.00	0.00
$\mu(Y), \sigma$	6	-9,094.57	300.84	0.00	0.00
μ, σ (unimodal)	2	-8,965.53	429.88	0.00	0.00

estimated for 2015–2018 were very similar; post hoc models were added in which ω (or ω and μ_1) from 2014 differed from the other 4 years; however, these models were less parsimonious and the full model was selected (Table 1). Estimates of μ_1 (the size of oocytes in snow crab that had extruded that year) were highest in 2014, with the other years being about 9% smaller (Table 2). Supplement 2 illustrates the slight difference in oocyte area for 2015–2018, shown with the average cutoff. We calculated the cutoff point in oocyte size between year-1 spawners and year-2 biennial spawners for each year (Table 2). There was very little variance among years, and the average cutoff across all years was identical to the cutoff estimated for 2014 (0.158 mm²). We used the average cutoff in all

years to identify which snow crabs were likely biennial year-2 spawners; when compared with using unique cutoffs for each year, there was only a single snow crab whose status changed.

In 2014, two models explained the probability of a snow crab being a biennial year-2 spawner nearly equally well (Table 3). In both models, the probability of a snow crab being a biennial year-2 spawner was heavily influenced by SC, with SC2 snow crab having a 0% chance and SC3+ snow crab having an increased likelihood of being a biennial year-2 spawner. In the best-fit model, the probability varied among the three sampling locations, with the northern site exhibiting the highest proportion of biennial year-2 snow crab, the southern site having the

TABLE 2. The parameter estimates from the best-fit models in Table 1. The cutoff is the estimated cutoff in oocyte size (mm²) between first year and biennial year-2 snow crab calculated for each year.

Parameter estimates ± SE for best models						
Year	Varied among years		Same among years			Cutoff
	μ_1 (Y)	ω (Y)	σ_1	μ_2 (f)	σ_2 (f)	
2014	0.0919 ± 0.0018	0.0945 ± 0.0195	0.0266 ± 0.0004	0.188 ± 0.036	0.018 ± 0.0036	0.1580
2015	0.0731 ± 0.0011	0.0186 ± 0.0057				0.1564
2016	0.079 ± 0.0013	0.0163 ± 0.007				0.1605
2017	0.0773 ± 0.0013	0.0375 ± 0.0095				0.1554
2018	0.073 ± 0.0012	0.0096 ± 0.0045				0.1595

TABLE 3. Akaike information criterion values for models of the probability of a snow crab being a biennial year-2 spawner in 2014. The model column indicates the factors included in the model (see text for details), where Nul indicates the null model, Lat indicates latitude, CW indicates carapace width, T indicates bottom temperature with the number indicating the year of measurement, SC indicates shell condition, and Loc indicates location: southern, central, or northern eastern Bering Sea. The column heading *K* indicates the number of parameters in each model. The two best-fit models are indicated in bold italics.

Model	<i>K</i>	<i>AIC_c</i>	ΔAIC_c	Likelihood	<i>AIC_c</i> weight
<i>Loc, SC</i>	4	109.04	0.00	1.00	0.48
<i>Lat, SC</i>	4	111.00	1.96	0.38	0.18
Lat, T14, SC	6	113.06	4.02	0.13	0.06
Lat, T13, SC	6	113.07	4.03	0.13	0.06
Loc, CW, SC	6	113.22	4.18	0.12	0.06
Loc, T13, SC	6	113.22	4.18	0.12	0.06
Loc, T14, SC	6	113.22	4.18	0.12	0.06
Lat, CW, SC	6	114.72	5.68	0.06	0.03
CW, SC	4	123.97	14.93	0.00	0.00
SC	3	126.52	17.49	0.00	0.00
Lat, CW	5	136.80	27.76	0.00	0.00
Loc, CW	5	137.65	28.61	0.00	0.00
CW	3	143.18	34.14	0.00	0.00
Loc	3	143.61	34.57	0.00	0.00
Lat	3	144.60	35.56	0.00	0.00
Loc, T14	5	147.76	38.72	0.00	0.00
Loc, T13	5	147.76	38.72	0.00	0.00
T14	3	163.57	54.53	0.00	0.00
Nul	1	164.35	55.31	0.00	0.00
T13	3	168.03	59.00	0.00	0.00

lowest (essentially 0), and the central site being intermediate between the two. In the second best-fit model (ΔAIC_c of 1.96), the probability varied with latitude. Parameter estimates show two different ways of describing the same pattern of an increasing probability of being biennial with increasing latitude (Table 4). Models that included CW and NBT (both at the year of capture and the previous

TABLE 4. Parameter estimates for the two best-fit models from Table 3.

Best-fit models	Parameter estimates ± SE
Lat, SC	
<i>P_{max}</i> (SC3+)	0.676 ± 0.112
<i>P_{max}</i> (SC2)	0.00 ± 0.00
<i>Lat</i> ₅₀	60.4 ± 0.049
<i>b_{Lat}</i>	-95.1 ± 19.4
Loc, SC	
<i>P_S</i>	0.00 ± 0.00
<i>P_C</i>	0.124 ± 0.035
<i>P_N</i>	0.560 ± 0.099
<i>c_{SC2}</i>	0.00 ± 0.00

year) in addition to SC and latitude were less parsimonious than those without. The Pearson’s correlation matrix (Supplement 3) shows strong association between CW and latitude, and latitude and NBT in 2014, while only moderate to low correlation between CW and NBT in 2013 and 2014.

Examining only SC3+ females sampled inclusive of this study, 21.2% of the SC3+ snow crab sampled at selected index sites in 2014 were estimated to be biennial year-2 spawners, which was notably higher than estimates derived for subsequent years (1.3% to 3.4%; Table 5). The number of SC3+ females determined to be biennial year-2 spawners remained unchanged when year-specific cutoff estimates were used, and therefore the average cutoff across years was used in our analyses. There was a 2.5–8-fold decrease in the proportion of year-2 biennial snow crab in 2015–2018 compared with 2014, as shown by the mixing parameter (ω). The population-level weighted estimates calculated for 2015–2018 ranged from 0.08% to 1.55% (Table 5). Figure 2 displays the proportions of SC3+ snow crab that are on annual or year-1 biennial and year-2 biennial reproductive cycles alongside NBT from the summer NMFS bottom trawl survey for 2014–2018. In general, snow crab identified as biennial year-2

TABLE 5. Variation in the number and percent of both annual or biennial year-1 and biennial year-2 (shell condition 3+ [SC3+]) female snow crab sampled in the eastern Bering Sea and estimated percent of the population that was second-year biennial spawners. No weighted average was calculated for 2014 due to the sampling design in that year; all other years include the weighted average \pm SD by population abundance for all stations where SC3+ snow crab were sampled for this study.

Sample	2014	2015	2016	2017	2018
Biennial year-2 spawners sampled (number)	25	11	2	2	4
Annual/biennial year-1 spawners sampled (number)	93	345	56	158	198
Biennial year-2 spawners sampled (%)	21.2	3.1	3.4	1.3	2.0
Percent of population biennial year-2 spawners (%; weighted average \pm SD)		0.36 \pm 0.03	0.08 \pm 0.02	1.55 \pm 0.07	0.19 \pm 0.01

spawners were observed in colder, more northern areas in the eastern Bering Sea.

All data and R code used in this project are available and will be supplied upon reasonable request.

DISCUSSION

In this study, we utilized oocyte area in an effort to distinguish annual and biennial year-1 snow crab from biennial year-2 snow crab captured in the eastern Bering Sea survey. Oocyte area exhibited the predicted bimodal distribution expected when two different reproductive cycles are present. Over all years sampled, only 1.4% of SC2 snow crab had oocyte areas that placed them in the biennial year-2 category, as is anticipated if larger oocytes represent snow crab in the second year of a biennial reproductive cycle. In addition, the proportion of snow crab that reproduce biennially varied with latitude and among years, with temperature likely as the most probable driver.

Developing a method to evaluate biennial spawning on the eastern Bering Sea survey was a critical aspect of this project because the survey is the only platform that can be practically and reliably used to collect data on biennial spawners. The bimodal distribution of oocyte area provides a potentially useful metric to distinguish biennial spawning that is mechanistically consistent with our understanding of snow crab reproductive cycles and matches ovarian and oocyte development in populations of snow crab believed to be all annual or biennial spawners (Ito 1963; Kanno 1987; Sainte-Marie 1993). The validity of the method is indirectly supported by the low rate (1.4%) at which SC2 snow crab, which should have extruded clutches within the previous few months, were classified as biennial year-2 spawners. Given the mean and standard deviation of the smaller mode in 2014 and a cutoff of 0.158 mm², 0.7% of snow crab in the lower mode are predicted to be above the cutoff and thus erroneously classified as biennial year-2 spawners. This expected error rate alone could fully account for the number of SC2 snow crabs identified as biennial year-2 spawners and any remainder could be the result of incorrectly assigned SC

codes as SC codes are somewhat subjective and result in misclassification; mature female SC2 snow crab are unlikely to be classified as SC3 given the short time since molting, but the reverse may occasionally happen, particularly in cold waters where the growth of epiphytes, one of the indicators of older-shell snow crabs, is slow and the potential for biennial spawning is high (Ernst et al. 2005). Our assessment of biennial spawning hinges on the key operational assumption that oocyte area is a reliable means for distinguishing reproductive cycle length. Blue king crab *Paralithodes platypus* also undergo a biennial reproductive cycle, with females brooding a clutch of eggs for a year prior to hatching (Somerton and Macintosh 1985). The females are then barren for a second year before they molt and extrude a new clutch. Oocyte size in the population exhibits a bimodal distribution in size, with brooding females having oocytes in the small mode and barren females in the larger, indicating that oogenesis progresses throughout the 2-year cycle (Somerton and Macintosh 1985). This is similar to what we observed here, except that for snow crab the females are brooding eggs for the full 2 years.

On the other hand, if bimodality of oocyte area resulted from factors other than the difference in 1- and 2-year reproductive cycles, then our method would be unreliable. Nonetheless, variation in lipid content, crab condition, location of oocytes in the ovaries, or other factors that could confound our results seem unlikely to explain the doubling in oocyte size that we documented but would more likely contribute to increased variation around a single mean rather than a bimodal distribution. A dedicated lab-holding study of ovigerous females is recommended, where oocyte size can be examined throughout 1- and 2-year development, and will be necessary to unambiguously demonstrate that oocyte size can be used to distinguish between females in their first and second years of brooding. Another possibility that could explain the bimodality in the oocyte sizes is that primiparous crabs generally mate in January and multiparous crabs several months later. Thus primiparous crabs could have larger oocytes when sampled in July. If this were the case, however, the snow crab in the

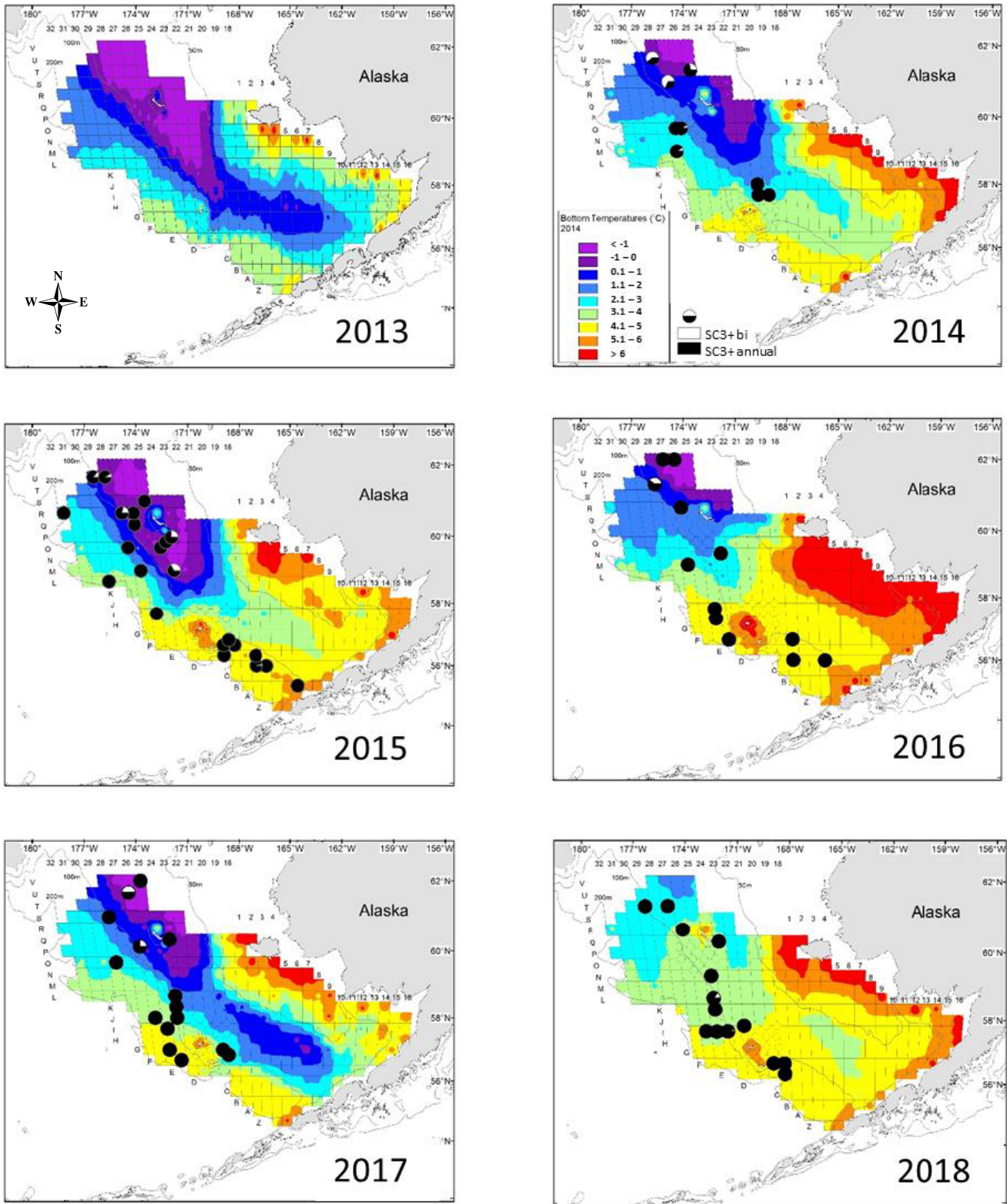


FIGURE 2. Proportions of annual and year-1 biennial (black) and year-2 biennial (white) female snow crab (shell condition 3+) shown across 2014–2018 near-bottom temperatures from the National Marine Fisheries Service bottom trawl survey occurring May–August. Near-bottom temperatures are also shown for 2013.

larger mode would all be SC2 and those in the smaller mode would be SC3+, which is the opposite of what we observe. Indeed, when we fit the data from all years and allowed both modes to vary, we estimated μ_1 and μ_2 values of 0.071 and 0.114 mm², respectively. This could be due to the difference between primiparous and multiparous females, although it would be very difficult to show this given the large overlap in the two distributions. Further, in both annual and biennial spawning populations, GSI, which is correlated with oocyte size, cannot be used to distinguish between primiparous and multiparous spawners (Ito 1963; Sainte-Marie 1993). Considering all this, the most likely explanation for the bimodality in the oocyte data is the difference between biennial and annual spawners in time since oocyte development began; however, a laboratory study to examine oocyte development in confirmed annual and biennial snow crab is needed to confirm our assumptions. In successive population-level studies in the eastern Bering Sea, sampling should also focus on only SC3+ snow crab, which should increase statistical power by eliminating SC2 snow crab that can be reasonably assumed to all be in the first year of their first reproductive cycle.

The rate of biennial spawning in the eastern Bering Sea derived by these methods varied both spatially and among years, with the latitudinal gradient in temperature (north-south) and interannual temperature differences likely as the primary cause, despite the fact that eastern Bering Sea bottom temperatures were a poor predictor of biennial spawning (see discussion below). The proportion of year-2 biennial snow crab was 2.5–8 fold lower in 2015–2018 than in 2014. This matches well with large-scale trends in bottom water temperature in the eastern Bering Sea. The years 2014–2018 were associated with an unusually warm phase in the eastern Bering Sea (Stabeno et al. 2018), which followed a long series of colder years (2007–2013). While the 0–2°C portion of the cold pool extended further south in 2017 compared with other years we sampled (Figure 2), 2017 is still considered a “warm” year based on the 30-year average for the eastern Bering Sea. Colder water temperatures in 2013 (Figure 2) likely led to the higher estimate of biennial year-2 snow crab in 2014; biennial reproduction would have been triggered when embryos were extruded in the colder water in 2013. We note that differences in our sampling design between 2014 and all subsequent years of study saw disproportionate sampling in the north of the eastern Bering Sea survey grid in 2014 and warrant a cautionary approach in making interannual inferences.

The exact timing when temperature dictates a change in cycle length is unknown; however, the work of both Moriyasu and Lanteigne (1998) and Webb et al. (2007) indicates that temperatures soon after embryo extrusion (i.e., late winter–early spring) determine whether an extended period of diapause is induced, thus initiating a

biennial cycle. Prior lab studies have also shown plasticity of initial embryo stage transitions, consistent with the hypothesis of early postextrusion temperatures acting as a primary mechanism activating biennial spawning, while finding more “locked-in” developmental pathways further along in embryo development (Kuhn and Choi 2011). In 2015–2018 oocyte development and embryo extrusion would have occurred under warmer bottom temperature conditions, which likely explains the very low proportion of biennial year-2 snow crab. We emphasize that Table 5 reports only the numbers of biennial year-2 spawners and not total biennial spawning. If one assumes that the proportion of the stock that is biennial year 1 in a given year is the same as the proportion that is biennial year 2 the next, one could estimate the total proportion in each year by adding the proportions in two subsequent years; however, further work to expound on the environmental pressures acting on spawning are required.

Although temperature at or shortly after extrusion is likely what mediates between biennial and annual cycles in snow crab (Webb et al. 2007), temperature during the eastern Bering Sea survey was a relatively poor predictor of biennial spawning. Survey temperature data only provide a snapshot of the thermal history of a snow crab: the temperature experienced by an ovigerous female at least 3 months postextrusion for annual and biennial year-1 snow crab and at least 15 months postextrusion for biennial year-2 snow crab. Caution is warranted in inferring a straightforward link between eastern Bering Sea NMFS survey temperature data and biennial reproduction for the Bering Sea. Prior studies have sampled both annual and biennial spawners simultaneously at individual sites where either cold or warm temperatures dominated (Rugolo et al. 2005; Kolts et al. 2015), suggesting that temperature at the time of capture may not be an adequate metric to deduce reproductive cycle. Murphy et al. (2017) developed an egg production index to better characterize the complex female components of the eastern Bering Sea snow crab stock, accounting for such differences as per-capita fecundity by reproductive stage and annual and biennial spawning. To categorize mature females as either annual or biennial spawners, they used summer bottom temperatures from the eastern Bering Sea NMFS survey as a proxy to distinguish between the two cycle durations. The study assumed that the available temperature data would be indicative of cycle length and employed a 1°C threshold to divide historical ovigerous female population data. Our results put several of their assumptions into question, and we strongly suggest that their threshold was too high and, therefore, estimates of the effect of biennial cycles were as well, although more data will be required incorporating population-level estimates from colder years to suggest a better threshold and more accurate population-level estimates.

Because size at maturity in snow crab is positively correlated with lifetime thermal exposure (Burmeister and Sainte-Marie 2010; Dawe et al. 2012), we hypothesized that small size might also be correlated with higher rates of biennial spawning. Consistent with this, we found a negative correlation between the size of mature females and latitude (Supplement 3). However, CW was, similar to eastern Bering Sea NBT, a poor predictor of biennial reproductive cycles. Neither of these variables, it seems, strongly correlate with the temperature exposure during the critical period soon after embryo extrusion.

The lack of correlation between these direct (both NBT in the year of capture and previous year) and indirect measurements of temperature and biennial spawning is likely caused by snow crab movement. Mature female snow crab in the eastern Bering Sea exhibit an ontogenetic migration in a general southwest direction, presumably following temperature gradients along the eastern Bering Sea shelf (Parada et al. 2010). The biennial year-2 snow crab in this study experienced conditions that triggered a 2-year cycle 15–19 months prior to their capture. The average migration of a mature snow crab transitioning from the primiparous to multiparous stage can exceed 70 nautical miles over a single year, and migration direction and distance vary among individual snow crab and among regions throughout the eastern Bering Sea (Ernst et al. 2005). Tracking data available for male snow crab shows considerable variance in movement rates and direction for individuals (Nichol and Somerton 2017). Accurately backtracking ontogenetic migration for individual snow crab to estimate the location and temperature at extrusion is not feasible given the absence of data on the movements of females.

Although survey temperatures proved to be a poor predictor, biennial spawning in female snow crab generally increased with latitude. In 2014, latitude and location were the best predictors of the proportion of snow crab that were identified as biennial year-2 spawners. Although biennial year-2 snow crab were rare in subsequent years, a higher rate of biennial spawning was still visually apparent at higher latitudes (Figure 2). Given the negative correlation between temperatures and latitude (Figure 2; Supplement 3) and the southwestern migration of mature females, there is a high likelihood that snow crab captured in the northern portions of the survey area have inhabited colder waters during the previous year than snow crab in the south. This pattern is consistent with the idea that lower temperatures are an important cause of biennial spawning.

The differences in oocyte development among years are less easy to explain. Oocyte size in females in the first year of their reproductive cycles was about 9% smaller in 2015–2018 than in 2014. This is the opposite of what one might expect because hatching, and subsequent extrusion,

is likely to occur earlier in warmer years than in cooler (Fusaro 1980). Thus, in warmer years the new oocytes would theoretically have had longer to develop than in a cooler year. It could be that in warmer years, basal metabolism in the females is higher, leaving less energy to commit to reproduction (Haddon and Wear 1993). This warrants future investigation to discover if temperature affects oocyte development in a way that could carry over to later life history stages. Carryover effects could include a reduction in the viability and health of snow crab embryos and larvae, as was documented for Tanner crab following exposure to low-pH water during oogenesis (Long and Swiney 2016; Swiney and Long 2016).

A better understanding of female reproduction can help managers better understand a stock and predict how environmental variables might change productivity. For example, changes in egg production provide insight into the effects of exploitation by fishing or impacts from the environment (Orensanz et al. 1998; Fischer and Thatje 2008). For species with highly variable reproductive output, the development of reference points may benefit to integrate the variables that regulate reproductive potential (Morgan et al. 2011); however, improving stock performance through the addition of female considerations is not guaranteed. Indeed, the Washington Dungeness crab fishery ignores the female component of the stock yet shows considerable resilience and sustainable yields despite high exploitation of males (Richerson and Punt 2020).

Although female snow crab are not harvested in the eastern Bering Sea, this portion of the stock still determines the upper limit of the stock's reproductive potential. Given the importance of reproductive potential on the longevity of a stock, female-specific reference points merit consideration when formulating management strategies for commercially exploited crustacean stocks, including those that target males only (Kruse 1993; Smith and Sainte-Marie 2004). Updating reference points to include egg production indices that account for missing female data can provide us more accurate reflections of the demographic variability and biological complexity of the stock (Kell et al. 2016). Although we may not anticipate estimates to diverge considerably from those using only mature-male biomass, the inclusion of female data, such as annual and biennial spawning proportions, into reference points underscores the importance of evaluating more complex management strategies that incorporate demographic features of reproductive potential and are robust to uncertainty (Morgan et al. 2011; Murphy et al. 2017). Although the rates of biennial spawning in the warm years of our study were low enough to be negligible, data from 2014 suggests that biennial reproduction triggered in colder years could reduce overall stock reproductive potential independently of mature-male biomass. Such interannual variability in the proportion of mature females

on a biennial reproductive cycle changes the effective sex ratio and the stock reproductive output, both of which have implications for the management of this stock (e.g., Zheng and Kruse 2003).

Conclusion

In this study, we estimated the proportion of biennially spawning snow crab in the eastern Bering Sea, which could contribute to the development of estimates of female reproductive potential (Szuwalski 2020) and female-based reference points. We recommend that future work include process studies that verify our assumptions on the relationship between oocyte size and biennial spawning. Targeted studies to elucidate the interaction between timing of temperature exposure and reproductive cycle length will help researchers and managers to know what temperature data is most useful, facilitating the use of model estimates of bottom temperatures in relation to female location to produce stronger egg production estimates. Elucidation of these unknowns would strengthen our understanding of spawner-per-recruit relationships and illuminate whether there is utility in incorporating female-specific biological reference points into current management strategies.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.