



**Abstract**—The red king crab (*Paralithodes camtschaticus*) is an important commercial fishery species in Bristol Bay in southwestern Alaska. Mature male biomass is used currently in assessment of this stock as an estimate of stock reproductive potential, but assessments can be improved by directly incorporating female reproductive potential. The climate of the Bering Sea oscillates between warm and cold stanzas, which have important consequences for the ecosystem in this area. With this study, we have added to previous work quantifying the relationship between size and fecundity of females, by examining whether thermal regimes affect reproductive output. Egg clutches were collected in 8 different years spanning warm and cold stanzas, and the fecundity during each year was determined. Although we found small differences in the relationship between size and fecundity among years, the relationship did not differ between warm and cold years. Average embryo dry mass was slightly different among years but not between warm and cold years. Additionally, the relationship between residual fecundity and average egg mass was negative, indicating that some variance in fecundity is driven by trade-offs between embryo size and number. We present a size–fecundity model for Bristol Bay red king crab that could be used to estimate reproductive output from the annual survey of the population of red king crab in Bristol Bay and could be incorporated into stock assessments in the future.

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## Reproductive potential of red king crab (*Paralithodes camtschaticus*) across warm and cold stanzas in Bristol Bay in southwestern Alaska

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Quantifying the reproductive potential of a stock is a critical element for fisheries management. Historically one of the most valuable fisheries in the United States (Bowers<sup>1</sup>), the fishery for red king crab (*Paralithodes camtschaticus*) in Bristol Bay, in southwestern Alaska, was closed in 2021 and 2022 because of low numbers of mature females after a massive decline. Although total female abundance is considered in the assessment and management process, this measure is coarse and fails to account for variance in egg production due to factors such as female size, age, and environmental effects on fecundity (Palof, 2023). Male reproductive potential, which is used in the stock

assessment model for Bristol Bay red king crab (Palof, 2023), refers to the number of mature males multiplied by the estimated number of females they can fertilize within a mating season. With this approach, any direct estimate of egg production is eschewed in the stock assessment for Bristol Bay red king crab (Swiney et al., 2012).

Fecundity, or embryo production, has been suggested as an improved measure of reproductive potential (Bell<sup>2</sup>; Caputi<sup>3</sup>). One of the main reasons that spawning stock biomass is used as a proxy for reproductive potential for some fisheries stocks, including for the state of Alaska's management of red king crab, is that it is easy to estimate.

<sup>1</sup> Bowers, F. R., M. Schwenzfeier, S. Coleman, B. Failor-Rounds, K. Milani, K. Herring, M. Salmon, and M. Albert. 2008. Annual management report for the commercial and subsistence shellfish fisheries of the Aleutian Islands, Bering Sea and the Westward Region's shellfish observer program, 2006, 230 p. Alsk. Dep. Fish Game, Fish. Manage. Rep. 08-02. [Available from Alsk. Dep. Fish Game, P.O. Box 115526, Juneau, AK 99811-5526.]

<sup>2</sup> Bell, M. C. 2006. Review of Alaska crab overfishing definitions: 24–28 April 2006, Seattle, Washington. Report to the University of Miami Independent System for Peer Reviews, 29 p. [Available from [website](#).]

<sup>3</sup> Caputi, N. 2006. Alaskan crab overfishing definitions review: Seattle, Washington, 24–28 April 2006, 17 p. Report by the University of Miami Center for Independent Experts for the NOAA Alaska Fisheries Science Center. [Available from [website](#).]

Clutch fullness (CF), a qualitative estimate of relative clutch size traditionally estimated for lithodid crab species (Donaldson and Byersdorfer, 2005), is a poor estimator of relative fecundity (Swiney et al., 2010). To incorporate female reproductive potential into the management process, it is essential to quantify the functional relationships affecting embryo production and any underlying variability in fecundity (Swiney et al., 2012) due to female size, reproductive status, interannual variability, or environmental variability.

In Bristol Bay, male red king crab mate with soft-shelled females over a 5-month period that varies interannually but usually occurs from the end of January through June (Otto, 1990). Females must mate each year to produce an egg clutch as they cannot store sperm (Powell and Nickerson, 1965). Females molt and, within a span from hours to a few days, extrude eggs, which males fertilize externally; these embryos are brooded for 10–12 months prior to hatching (Powell and Nickerson, 1965; Stevens and Swiney, 2007). Fecundity of red king crab increases with female size (Otto et al., 1990), although there is evidence of declining fecundity as females approach senescence (Swiney et al., 2012). Fecundity is also lower in primiparous females, those brooding their first clutch of embryos, than in multiparous females, those brooding their second or later clutches (Swiney and Long, 2015). Although interannual variability in fecundity is low (Swiney et al., 2012), the potential effects of thermal variability remain unknown. Several aspects of the reproductive biology of red king crab, including the timing of molting and mating, duration of embryonic development, and ultimately hatch timing, depend on presiding water temperatures (Shirley et al., 1990; Stevens et al., 2008). In years with colder than average bottom water temperatures, embryonic development is prolonged and hatching and mating occur at later dates for multiparous females (Stevens et al., 2008; Chilton et al., 2010; Foy and Armistead, 2013).

In the Bering Sea, climatic oscillations occur at a decadal scale. Since the early 2000s, the eastern Bering Sea (EBS) has undergone multiyear stanzas characterized by either warm bottom water temperatures associated with low winter ice coverage (warm years or stanzas) or cold bottom temperatures with widespread winter ice coverage (cold years or stanzas) (Stabeno et al., 2012a, 2018). Mechanistically, the strength and position of the Aleutian low pressure system, tied to the Pacific Decadal Oscillation, influences winds and surface heat fluxes in the Bering Sea, in turn, affecting the formation, advection, and persistence of sea ice across the continental shelf of the Bering Sea (Stabeno et al., 2001) and the formation and extent of the cold pool (bottom water temperature  $<2^{\circ}\text{C}$ ). These oscillating climate stanzas affect the ecosystem, altering primary production and food supply to both pelagic and benthic communities, causing spatial shifts in stock distribution, and changing growth and molt timing in commercial fish and crab species (Orensanz et al., 2004; Mueter and Litzow, 2008; Stabeno et al., 2012b; Copeman et al., 2021). Although the bottom water temperatures in Bristol Bay during warm years are well within the

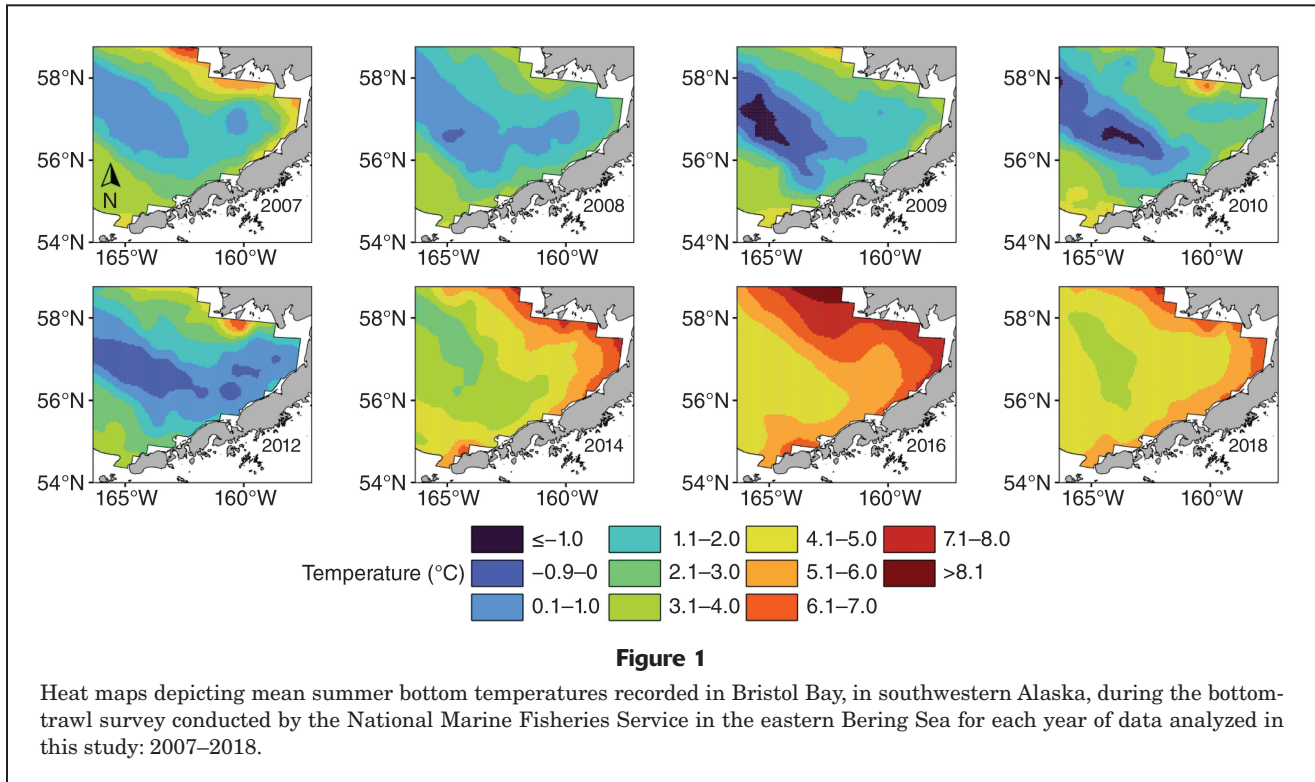
thermal tolerance limits of female red king crab and their embryos (Nakanishi, 1987; Shirley et al., 1990), it is conceivable that maternal reproductive investment could differ between these thermal stanzas because of either direct effects of temperature on crab energetics or indirect effects of food availability.

Previous studies of interannual variability in fecundity for female red king crab occurred solely in cold years in the EBS (Swiney et al., 2012; Swiney and Long, 2015). In our study, we compared previously published data on fecundity of Bristol Bay red king crab from cold years (2007–2012) with newly collected data from a set of warm years (2014–2018) (Stabeno et al., 2012a; Stabeno and Bell, 2019). This work allowed us to assess whether large-scale thermal stanzas lead to differences in reproductive investment by female red king crab in Bristol Bay, in terms of changes either to the relationship between size and fecundity or to embryo size, and allowed us to examine if trade-offs between embryo size and fecundity have differed among warm and cold years. In addition, we examined if and to what degree CF can be used to predict relative fecundity. The results of this study provide improved inputs needed to develop a more accurate model of stock reproductive potential based on female fecundity for Bristol Bay red king crab.

## Materials and methods

For the purposes of this study, we classified years prior to 2014 as cold years and the years 2014–2018 as warm years on the basis of the extent of the cold pool during the bottom-trawl survey conducted in the EBS by the National Marine Fisheries Service (NMFS) (Fig. 1) and the mean bottom temperature experienced by ovigerous red king crab in Bristol Bay (weighted mean temperature) and recorded during the summer NMFS EBS bottom-trawl survey. Bristol Bay is defined in our study as king crab Registration Area T, which is the area south of  $58^{\circ}39'N$ , north of  $58^{\circ}36'N$ , and east of  $168^{\circ}W$  established for vessel registration and fishing regulation (Registration . . . 2024). This area comprises 54,536 square nautical miles ( $\text{nmi}^2$ ) and, for the NMFS EBS bottom-trawl survey, is separated into 136 stations, with each station having an area of approximately  $400 \text{ nmi}^2$  (Zacher et al., 2023). In cold years, the cold pool extended into Bristol Bay, and the weighted mean temperature was below  $4^{\circ}\text{C}$  (Table 1). Annual weighted mean bottom temperatures experienced by female red king crab in Bristol Bay were calculated by weighting station bottom temperatures by the mature female catch per unit of effort at that station and averaging this value across stations with a positive catch of red king crab (Table 1).

Egg clutches of ovigerous red king crab were collected from Bristol Bay (Zacher et al., 2023) during the NMFS EBS bottom-trawl surveys conducted in summer (Lang et al., 2019). Collection methods in 2014, 2016, and 2018 mirrored those used in 2007–2010 and in 2012 and described in Swiney et al. (2012). In summary, ovigerous

**Table 1**

Number of female red king crab (*Paralithodes camtschaticus*) sampled from Bristol Bay, in southwestern Alaska, during bottom-trawl surveys from 2007 through 2018 and mean bottom water temperatures at survey stations weighted by female abundance. Females were sampled to generate length-based fecundity estimates.

Year	No. of samples	Mean temperature (°C)
2007	135	3.04
2008	147	3.26
2009	133	2.67
2010	137	3.24
2012	145	2.80
2014	151	4.62
2016	146	5.33
2018	126	4.56

females were haphazardly sampled from the bottom-trawl survey until 20 clutches of recently extruded embryos (i.e., no eyes were visible on the eggs) per 10-mm size bin, with carapace lengths (CLs) between 70 and 140 mm, were collected. Twenty clutches were also collected from females with a CL greater than 150 mm. Samples were frozen at sea. For each female, CL and CF were recorded. Clutch fullness was assessed and visually approximated on a 6-point scale: 6 for a 100% full clutch,

5 for a clutch 75% full, 4 for a clutch 50% full, 3 for a clutch 25% full, 2 for a clutch within the range from a trace of eggs to a clutch 12.5% full, and 1 for a mature crab with no eggs. Although egg volume is a continuous parameter, at-sea survey work necessitates a quick grading process for all ovigerous females encountered, and CF is converted to a categorical variable through visual approximation by the sampler. Mature crab with no eggs were differentiated from immature females on the basis of their ventral anatomy (i.e., the size of their abdominal flap) per Donaldson and Byersdorfer (2005). In immature females, the abdominal flap is small and the coxae of the walking legs are exposed, making immature females easy to distinguish from barren mature crab, whose abdominal flap entirely covers the first coxa. A total of 1118 female red king crab were sampled across 7 years and ranged in CL from 73 to 167 mm.

We estimated fecundity in the laboratory by using modified protocols from Otto et al. (1990). We gently stripped embryos off the pleopods, counted 2 random samples of 250 embryos, and dried these and the remaining embryos at 60°C until a constant mass was attained. Fecundity was calculated by dividing the total embryo dry mass by the average of the 2 individual estimates of embryo dry mass from the subsamples taken to determine total embryo count.

We estimated parameters for a series of models from the fecundity data by using maximum likelihood estimation and assuming a normal distribution of errors in the statistical program R, vers. 4.2.1 (R Core Team, 2022). Normality was checked by examining a histogram of residuals

from the best-fit model. For the base model, we assumed that fecundity would increase linearly with crab size:

$$F = mCL + b, \quad (1)$$

where  $F$  = fecundity in number of embryos;

$CL$  = carapace length in millimeters;

$m$  = the slope; and

$b$  = the intercept.

To model the change in the size–fecundity relationship due to senescence (Swiney et al., 2012), we incorporated a split-point regression in some of the models in which the slope of the relationship changes above a critical size:

$$\text{If } CL < Sp, \text{ then } m = m_1, \text{ or} \quad (2)$$

$$\text{If } CL \geq Sp, \text{ then } m = m_2, \quad (3)$$

where  $Sp$  = the CL at the split point in millimeters and was fit as a parameter.

To examine interannual differences, we included models in which the slope was a linear function of year (Swiney et al., 2012; Swiney and Long, 2015). Additionally, we included a model in which the slope in cold years was the same (2007–2012) and differed from the slope in warm years (2014–2018). To account for differences in CF, models were included as follows:

$$F = (mCL + b)(1 - D_{CF}), \quad (4)$$

where  $D_{CF}$  = a linear function of CF and represents the percent decrease in fecundity compared to that of a full (CF=6) clutch (i.e.,  $D=0$  for a CF of 6).

Because of the low sample size for females with CF of 1–3 (sample size  $[n]=10$ ), we combined data for females with CF of 2–4 for analyses.

Post hoc, we observed that slopes were similar among multiple years (2007, 2009, 2014, 2016, and 2018), as well as between 2010 and 2012. Therefore, we constructed an additional model in which those groups of years had identical slopes. Also, we observed that the  $D$  for a CF of 5 was indistinguishable from 0 ( $D_5=0.0038$  [standard error of the mean (SE) 0.0042]); therefore, we included an additional model where  $D$  for a CF of 6 and a CF of 5 were both 0. Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ) was calculated for each model and used to select the best-fit model. Models with a difference between  $AIC_c$  values that was less than 2 were considered to explain the data equally well (Burnham and Anderson, 2002).

Average individual embryo dry weights were examined by using an analysis of covariance (ANCOVA) with maternal size (CL) fully crossed with year. Differences in egg mass among levels of CF were examined by using a 2-way analysis of variance (ANOVA), with year and CF as factors. All ANCOVAs and ANOVAs were done in SYSTAT<sup>4</sup>, vers.

13.2.01 (Grafiti LLC, Palo Alto, CA), and the assumptions of normality and homogeneity of variance were verified by using the Shapiro–Wilk test (normality) and Levene's test (homogeneity of variance).

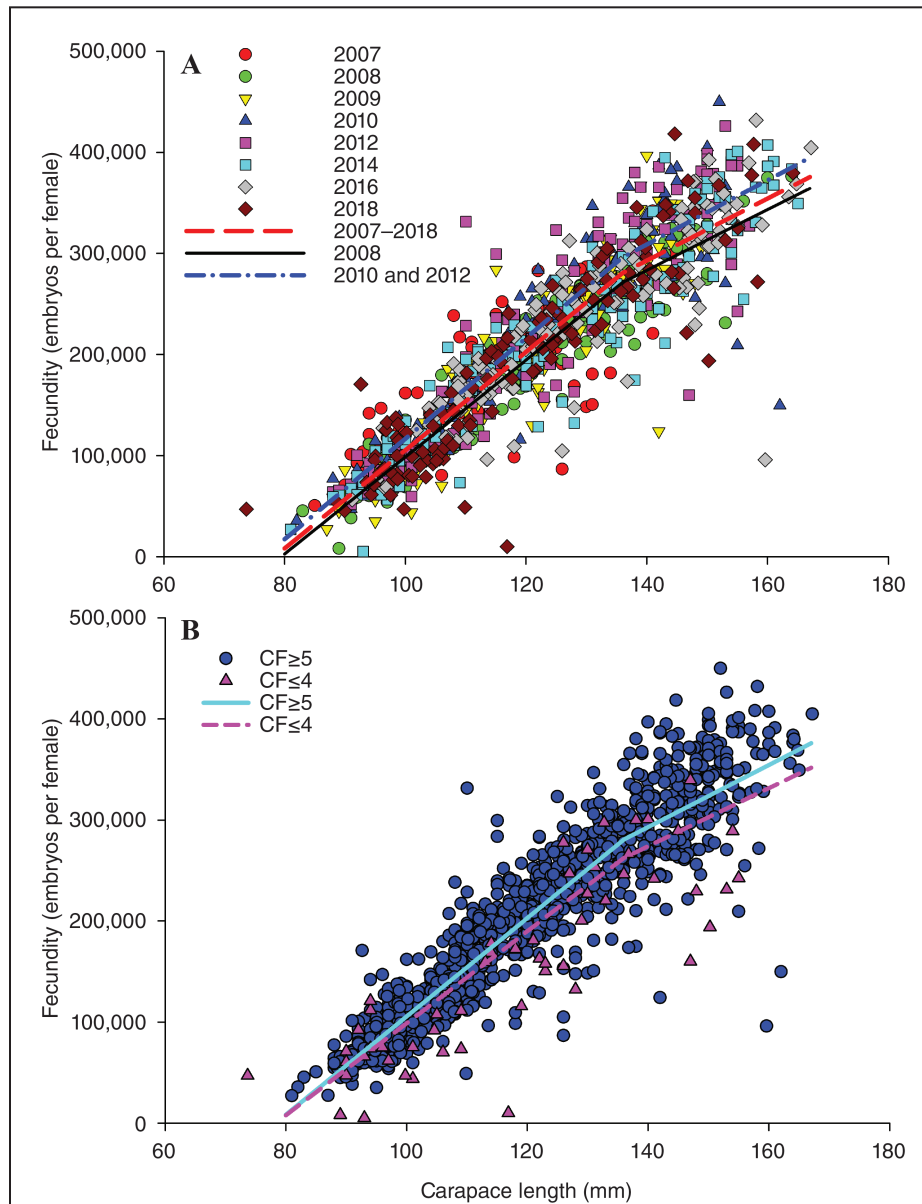
To examine potential trade-offs between embryo size and fecundity, we calculated the residual fecundity for each female by using the best-fitting model from the work described in the previous paragraph (i.e., the difference between the observed fecundity and the fecundity predicted by the model) and analyzed it with a fully-crossed ANCOVA with average embryo dry mass and year as factors.

## Results

Fecundity increased with female size and ranged from 5200 to 450,000 embryos (Fig. 2). In the best-fit model, the slope of the relationship between size and fecundity differed among years, with 2008 (cold year) having the lowest slope, 2007 and 2009 (cold years) and 2014, 2016, and 2018 (warm years) having the same, slightly higher slope, and 2010 and 2012 (cold years) pooled together having the highest slope (Table 2, Fig. 2). Additionally, the split point was allowed to vary, and for females with a CL above approximately 136 mm, the slope dropped (Table 3). Finally, fecundity was 6.5% lower for individuals with a CF of less than 5 compared to that for those with a CF of 5 or above, but there was no significant difference in fecundity between individuals with CFs of 5 and 6. There was no support for the model in which slopes differed between warm and cold years (Table 2). Differences in the size–fecundity relationship among years were small (Fig. 2, Table 3). The best model proved an excellent fit to the data, explaining 86% of the variance (Table 3).

To explicitly analyze the effect of temperature on fecundity, we regressed the slope estimates for each year (from the model in which the parameter slope is allowed to vary above a split point and among years and the other parameters are intercept and standard deviation; Table 2) against the weighted mean bottom temperature. The weighted mean temperature was derived by using data from the stations of the NMFS EBS bottom-trawl survey in Bristol Bay. Temperature had no effect on the slope of the size–fecundity relationship (linear regression:  $P=0.55$ ; [Suppl. Figure](#)). Although results from the best-fit model indicate clear differences in fecundity among the years for which data were examined, those differences were not caused by temperature and cannot be predicted from survey data analyzed in this study. To create a model that can be used to calculate estimated egg production from survey data, we fit a model that contained all the parameters in the best-fit model except those specific to year. Parameters for this model are provided in Table 3. Although the difference in  $AIC_c$  between this model and the best-fit model was 40.9 (indicating strong statistical support for differences among years), the difference in the coefficient of multiple determination ( $R^2$ ) between models was only 0.006, indicating that differences among years account only for 0.6% of the variance in the data.

<sup>4</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.



**Figure 2**

Comparisons of the relationship between size and fecundity for female red king crab (*Paralithodes camtschaticus*) collected in Bristol Bay in Alaska from 2007 through 2018, (A) among years and (B) between levels of clutch fullness (CF). Points represent the data for individual crab, and the lines represent the estimated trend from the best model. Fecundity was qualitatively estimated through visual approximation. In panel A, inter-annual comparisons are for red king crab visually estimated to possess egg clutches that were either 75% full (CF=5) or 100% full (CF=6), and the pink dashed line indicates the trend for the years 2007, 2009, 2014, 2016, and 2018. In panel B, comparisons are for 2007, 2009, 2014, 2016, and 2018 only. A CF designation of 4 indicates that crab had egg clutches that appeared 50% full.

Mean embryo dry mass was 201  $\mu\text{g}$  (SE 15) across all years. Although there was no pattern in variation of embryo dry mass with temperature stanzas, average embryo mass differed among years (ANCOVA:  $F=2269$ ,  $P=0.027$ ) with a 10% maximum difference (Fig. 3, [Suppl. Table](#)). Year and female size had an interactive effect

(ANCOVA:  $F_{7,1104}=2.32$ ,  $P=0.024$ ), indicating a violation of the assumption of homogeneity of slopes. Therefore, a linear regression between female CL and embryo mass was performed for each year separately. Embryo weights decreased with increasing maternal size for 3 of 8 years (2009, 2012, and 2016:  $P<0.03$ ; Fig. 3) but not for the other

**Table 2**

Models used to examine the relationship between size and fecundity for the stock of red king crab (*Paralithodes camtschaticus*) in Bristol Bay in southwestern Alaska. Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ) was used to identify the best-fit model. The difference in  $AIC_c$  between each model and the best model ( $\Delta AIC_c$ ) and  $AIC_c$  weights for each model are also presented.  $K$  indicates the number of parameters in each model. The model parameters include the slope ( $m$ ), intercept ( $b$ ), decrease in fecundity as a linear function of egg clutch fullness ( $D_{CF}$ ), and standard deviation ( $\sigma$ ). Models were fit to data from bottom-trawl surveys conducted in the eastern Bering Sea during 2007–2018. In several models, the slope is allowed to vary above a split point ( $Sp$ ) or to vary among years ( $Y$ ). In one model, slope is allowed to vary with the thermal regime ( $Y_T$ ; i.e., the slope differs between warm and cold years).  $Y^*$  indicates post-hoc models in which the slope parameter did not differ among groups of years (data for 2007, 2009, 2014, 2016, and 2018 were the same, and data for 2010 and 2012 were the same).  $D_{CF}^*$  indicates a post-hoc model in which  $D_{CF}$  did not differ between crab with clutch fullness scores of 6 (100% full clutch) and 5 (75% full clutch).

Model	$K$	$AIC_c$	$\Delta AIC_c$	Likelihood	$AIC_c$ weight
$m, b, \sigma$	3	26,566.33	122.73	0.00	0.00
$m(Sp), b, \sigma$	5	26,529.35	85.75	0.00	0.00
$m(Y), b, \sigma$	10	26,536.10	92.50	0.00	0.00
$m(Y, Sp), b, \sigma$	12	26,498.65	55.05	0.00	0.00
$m(Y_T, Sp), b, \sigma$	6	26,528.45	84.85	0.00	0.00
$m(Y^*, Sp), b, \sigma$	7	26,488.38	44.78	0.00	0.00
$m(Y^*, Sp), b, D_{CF}, \sigma$	9	26,444.89	1.29	0.52	0.34
$m(Y^*, Sp), b, D_{CF}^*, \sigma$	8	26,443.60	0.00	1.00	0.66

**Table 3**

Parameter estimates and goodness of fit for the best-fit model of the relationship between size and fecundity for the stock of red king crab (*Paralithodes camtschaticus*) in Bristol Bay in southwestern Alaska and for a model in which interannual differences were excluded (this model represents the best model that can be used for predicting fecundity with survey data). Standard errors are indicated parenthetically. Parameters include intercept ( $b$ ), slope ( $m$ ), change in slope ( $\Delta m$ ), carapace length at the split point in millimeters ( $Sp$ ), change in slope above the split point ( $\Delta m_{Sp}$ ), and proportional decrease in fecundity in crab with clutch fullness (CF) scores from 2 (from a trace of eggs to a 12.5% full clutch) to 4 (50% full clutch) ( $D_{CF2-4}$ ). For  $\Delta m$ , subscripts indicate if the change in slope is for particular years (2008 or 2010 and 2012) or above the split point ( $Sp$ ). Coefficients of multiple determination ( $R^2$ ) were used to determine goodness of fit. Models were fit to data from bottom-trawl surveys conducted in the eastern Bering Sea during 2007–2018.

Best-fit model		Model averaged across years	
Parameter	Estimate	Parameter	Estimate
$b$	-380,708 (10,362)	$b$	-376,173 (10,316)
$m$	4863 (92)	$m$	4840 (91)
$\Delta m_{08}$	-69 (27)		
$\Delta m_{10,12}$	114 (21)		
$Sp$	136.0 (2.6)	$Sp$	137.7 (2.5)
$\Delta m_{Sp}$	-1789 (329)	$\Delta m_{Sp}$	-1790 (330)
$D_{CF2-4}$	-0.065 (0.009)	$D_{CF2-4}$	-0.066 (0.010)
$R^2$	0.857	$R^2$	0.851

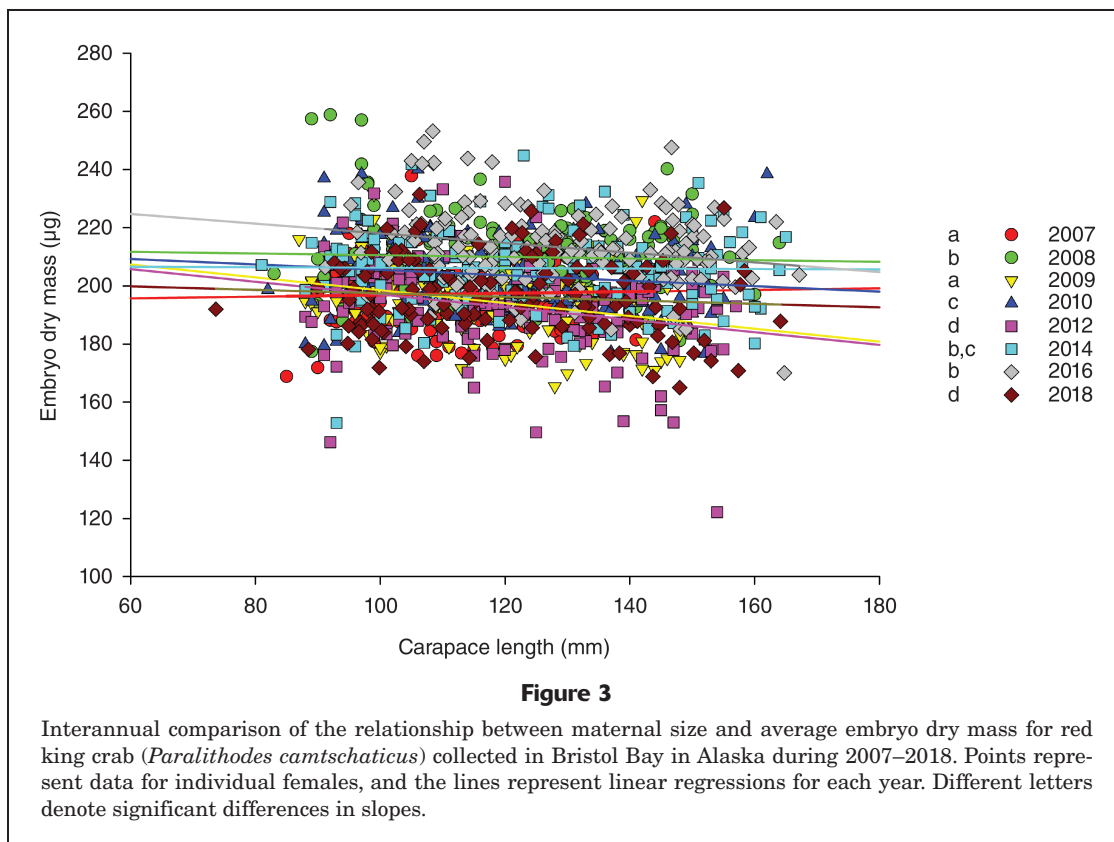
5 years (linear regression:  $P > 0.05$ ). The effect of female size for the years for which CL was significant was small, with the size of the effect ranging from 5.7% to 7.5% across the range of CLs predicted (Fig. 3), and the relationship disappeared when all years were analyzed together ( $P = 0.105$ ,  $R^2 = 0.002$ ) with a predicted 1.8% difference across the range of CLs. Residual fecundity decreased with average embryo mass (ANCOVA:  $F_{1,1094} = 64.412$ ,  $P < 0.0005$ ; Fig. 4) but did not differ among years ( $F_{7,1094} = 1.128$ ,  $P = 0.343$ ).

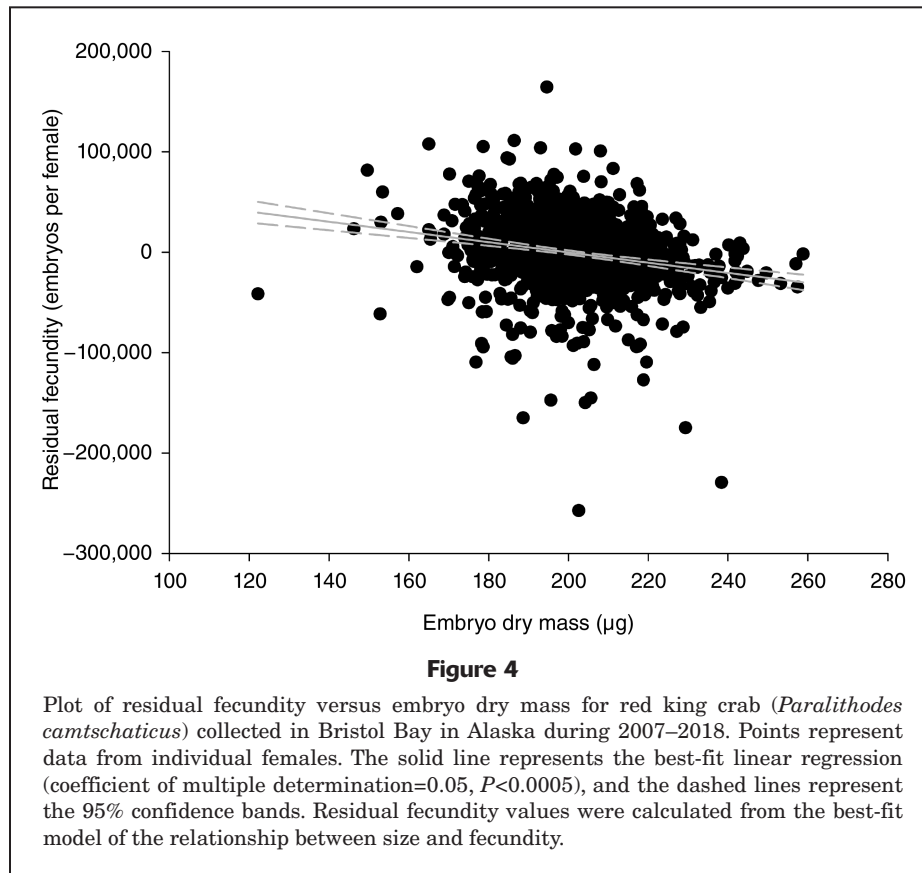
## Discussion

This study included the first examination of the reproductive output of females in the stock of red king crab in Bristol Bay across both warm and cold thermal stanzas in the EBS. Although there were slight differences among years in the relationship between size and fecundity, there were no differences between warm and cold years. Likewise, the average embryo dry mass differed among years; however, thermal stanza had no effect, indicating that temperature does not influence maternal investment per offspring. Although there is interannual variability in the relationship between size and fecundity that cannot be predicted with our best model, the interannual variability over the years studied was negligible, explaining less than 1% of the variance in the data. We confirm that the size–fecundity relationship decreased as size increased,

a trend likely attributable to senescence, but we will not discuss that further because it has been explored previously (Swiney et al., 2012). Average embryo dry mass decreased with residual fecundity, indicating a trade-off between embryo quality and quantity for this species; however, this relationship did not differ among years or between thermal stanzas. Overall, these data indicate that female reproductive potential for Bristol Bay red king crab was unaffected by interannual differences in water temperatures.

For Bristol Bay red king crab, there are a few mechanisms by which temperature might affect reproductive investment. Differences in benthic-pelagic coupling between warm and cold years could alter food quality and quantity for red king crab (Ramos et al., 2003; Copeman and Parrish, 2004; Richoux et al., 2004). Benthic productivity in the Bering Sea is highly correlated with ocean temperatures. In warm years, the spring bloom occurs later, and warmer temperatures increase pelagic secondary production, decreasing export to the benthos (Walsh and McRoy, 1986; Hunt and Stabeno, 2002). In contrast, in cold years, high flux from ice-edge and pelagic phytoplankton blooms increases the food quality and quantity reaching the benthos, benthic secondary production, and ultimately food quantity and quality for benthic predators (Wassmann and Reigstad, 2011; Grebmeier, 2012; Grebmeier et al., 2015). Both the quantity and quality of diet items significantly affect growth and lipid storage in juveniles of *Chionoecetes* species (Copeman et al., 2021),





and a similar response may be expected for ovigerous females of red king crab, resulting in reduced energy availability for reproduction.

A second mechanism that could cause differences in reproductive investment between warm and cold years is the direct effect of temperature on basal metabolic rates (Mauro and Mangum, 1982; Brill et al., 2015; Piatt et al., 2020). Reproductive processes, such as gonadal growth, gamete maturation, vitellus production, and aerating and cleaning the clutch, are all energetically demanding (Baeza and Fernández, 2002). Increased temperatures could raise metabolic demand and redirect energy from reproduction (Foyle et al., 1989; Pörtner et al., 2005; Copeman et al., 2021). Our data, however, offer no support for differences in reproductive investment with temperature. This result indicates that either the females were not food-limited and were able to consume more to compensate for a higher metabolic rate or, alternatively, they prioritized reproduction over other processes like somatic growth.

Future work should investigate whether there are any differences in the growth at molt or crab condition (e.g., lipid reserves) among thermal stanzas to address the second hypothesis regarding the mechanism of temperature. It is also possible that the temperatures females occupy during the NMFS EBS bottom-trawl survey are not representative of the thermal habitat occupied by ovigerous females throughout the year because of their migration

after the mating season. Current satellite tagging work on Bristol Bay red king crab combined with a new cooperative pot survey conducted in winter months in Bristol Bay will help improve understanding of the movement of females throughout the year.

Although we did not find an effect of thermal regime on the fecundity of Bristol Bay red king crab in our data, temperature plays an important role in the reproductive biology and growth of decapod crustaceans, manifesting through considerable variability in size–fecundity relationships that are specific to both species and region. The interaction of various environmental and biotic factors in different geographic areas may lead to different relationships between size and fecundity (Aiken and Waddy, 1988) or may influence interannual variation in a single area (Bagenal, 1973). The size–fecundity relationship for both American lobster (*Homarus americanus*) and European lobster (*Homarus gammarus*) varies regionally, and differences are most likely driven by temperature (Waddy and Aiken, 1991). Increases in temperature have likely caused a 23% decline in fecundity for female American lobster in southern New England due to increased egg loss (Goldstein et al., 2022).

However, a decline in fecundity is not necessarily correlated with rising temperatures. The size–fecundity relationship for the Australian spiny lobster (*Panulirus cygnus*) was the same in 2 regions with contrasting temperature extremes (Morgan, 1972). Similarly, Tully et al.



(2001) found no regional differences in the fecundity of European lobster between Ireland, the United Kingdom, and France, despite differences in temperature (they did not specifically test mean temperature as a covariate). In our study, temperatures in the warm years were still well within the thermal tolerance of red king crab and historic levels; however, if temperatures increase as predicted, it may be necessary to monitor Bristol Bay red king crab for reductions in reproductive potential. Mature red king crab from southeastern Alaska experience reduced growth at temperatures between 9°C and 12°C, and both mature females and embryos exhibit no change in mortality at temperatures up to 12°C (Shirley et al., 1990). However, thermal tolerance studies for Bristol Bay red king crab have been limited (Long and Daly, 2017). Lab-controlled studies are warranted to determine temperature thresholds for ovigerous red king crab in Bristol Bay and to determine the effects of increasing temperature on egg production and retention and on embryo development.

Embryo quality is an important component of reproduction and can directly affect offspring fitness. Allocation of energy into egg production can be both variable and adaptive, depending on the environment (Pond et al., 1996; Donelson et al., 2010; Shama et al., 2014), and embryo size is a metric of investment per offspring (Anger, 2001; Moran and McAlister, 2009). Two major resource allocations related to reproduction must be made. The first is energy allocation to reproduction (versus other metabolically demanding processes like somatic growth), and the second is energy allocation to each offspring. Two females may invest the same amount of energy into their clutches, but they will have different fecundities if their per-embryo investments differ (Giménez and Anger, 2003; Marshall and Keough, 2008).

Higher investment per embryo is often correlated with stressful environments and is likely an adaptation to increase the survival of offspring (Hartnoll et al., 2007; Jivoff et al., 2007; Firstater et al., 2012). In our study, embryo size was negatively correlated with residual fecundity for Bristol Bay red king crab (Fig. 4) but did not differ among years or thermal regimes. Although there were interannual differences in embryo weight, they did not differ among warm and cold years. For Dungeness crab (*Metacarcinus magister*), lower temperatures during embryogenesis were correlated with larger sizes at hatching (Shirley et al., 1987), highlighting the importance of examining species-specific maternal investment at various points in embryo development across time scales that capture variable thermal conditions.

Finally, this work establishes that the 6-point CF scale used on the NMFS EBS bottom-trawl survey has limited value. There was no statistical difference in fecundity at a given size between crab with 75% full clutches and crab with 100% full clutches (between crab with CFs of 5 and 6), and there was only a slight (6%) decrease in fecundity for crab with clutches that were 50% full or less (with CFs of 4 and below) in comparison to the fecundity of crab with CFs of 5 and 6, a decline that is surprisingly low given the differences in CF. Although our sample size was low ( $n=8$ )

for crab with CFs of 2–3, such individuals on average had 39% fewer eggs than the number of eggs predicted for a crab of the same size with a CF of 6. Two possible explanations are that individuals with a CF of 4 had smaller eggs, giving the appearance of a smaller clutch, or had a tighter packing density of their eggs. Of course, this idea would have to be substantiated through further study.

There was a significant difference in egg mass among levels of CF (2-way ANOVA:  $F_{4,1098}=4.054$ ,  $P=0.003$ ), with crab with CFs of 4 and 5 having smaller eggs than crab with a CF of 6. However, the effect size was small, with crab with CFs of 4 and 5 having eggs only 3.1% or 1.4% smaller than the eggs of crab with a CF of 6, respectively. These small differences are not sufficient to explain either a 25% or a 50% difference in estimated clutch volume. Mature female red king crab have a large size range, making estimation of relative versus absolute clutch size difficult and hard to standardize across multiple observers each year, and the morphology of the abdominal flap of red king crab contains no reference markers or accurate visual estimation of CF. All of these factors likely lead to substantial variation between observers in assessment of CF.

The differences in egg mass for crab with CFs of 4–6 confirm and add more data to support the idea that crab with CFs of 5 and 6 are more fecund than crab with a CF of 4 but not more than each other (Swiney et al., 2010). It is likely that the fecundity of crab with CFs of 2 and 3 is lower still (Donaldson and Byersdorfer, 2005). Crab with CFs of 2 and 3 are probably better categorized by observers than crab with higher levels of CF; however, it would take a focused study to collect sufficient crab to quantify the difference well given that only 5% of crab had a CF of 4 or below in our survey (Zacher et al., 2023).

## Conclusions

The primary objective for this multiyear study of the fecundity of Bristol Bay red king crab was to develop a model of the relationship between size and fecundity that incorporates ontogenetic differences (Swiney et al., 2012; Swiney and Long, 2015) and temperature variability (work described herein) to allow estimation of total stock reproductive potential to replace the estimation of male reproductive potential that is currently used in stock assessments. We present a highly accurate model that can be used to estimate total stock egg production from data on female abundance, clutch fullness, and size frequency collected during the NMFS EBS bottom-trawl survey. If future warming results in temperatures above those observed in this study, reevaluating the effects of temperature on fecundity and maternal investment may be necessary.

In future studies, researchers should model egg production across the survey time series, identify patterns over the time series, compare egg production to past metrics for stock reproductive potential, and evaluate the implications for stock assessment. Work in the future also should use the new estimate of egg production to examine the stock–recruit relationship for red king crab to update and

perhaps improve on previous analyses (Zheng and Kruse, 2000, 2003, 2006).

## Resumen

El cangrejo real rojo (*Paralithodes camtschaticus*) es una importante especie de pesca comercial en la bahía de Bristol, en el suroeste de Alaska. Actualmente, se utiliza la biomasa de machos maduros en la evaluación de esta población en la estimación de su potencial reproductivo, pero las evaluaciones pueden mejorarse incorporando directamente el potencial reproductivo de las hembras. El clima del Mar de Bering oscila entre estancias cálidas y frías, lo que tiene importantes consecuencias para el ecosistema de esta zona. Con este estudio, hemos complementado trabajos anteriores que cuantificaban la relación entre el tamaño y la fecundidad de las hembras, examinando si los regímenes térmicos afectan a la reproducción. Se colectaron lotes de desove de 8 años, abarcando temporadas cálidas y frías, y se determinó la fecundidad durante cada año. Aunque encontramos pequeñas diferencias en la relación entre tamaño y fecundidad entre años, la relación no difirió entre años cálidos y fríos. La masa seca media de los embriones varió ligeramente de un año a otro, pero no entre los años cálidos y los fríos. Además, la relación entre la fecundidad residual y la masa media de huevos fue negativa, lo que indica que parte de la varianza en la fecundidad se debe al equilibrio entre el tamaño y el número de embriones. Presentamos un modelo de tamaño-fecundidad para el cangrejo real rojo de la Bahía de Bristol que podría utilizarse para estimar la producción reproductora a partir del estudio anual su población en la Bahía de Bristol y podría incorporarse en futuras evaluaciones poblacionales.

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