Energetic limitations and mass mortality of Bering Sea snow crab: Interacting effects of warming and density on collapse and recovery

Erin J. Fedewa[1*], Louise A. Copeman[2] and Michael A. Litzow[1]

[1]Alaska Fisheries Science Center, National Marine Fisheries Service, 301 Research Court, Kodiak, AK 99615, USA

[2]Alaska Fisheries Science Center, National Marine Fisheries Service, 2030 SE Marine Science Dr., Newport, OR 97365, USA

*Corresponding author: erin.fedewa@noaa.gov

ORCHID IDs

Erin J. Fedewa: 0009-0009-4965-8886

Louise A. Copeman: 0000-0002-8851-7586

Michael A. Litzow: 0000-0003-1611-4881

ABSTRACT

Marine heatwaves can result in mass mortality events, but the mechanisms underlying population collapse and recovery dynamics are often poorly understood. Here, we employed a comparative analysis between collapsing and non-collapsing portions of the Bering Sea snow crab population to evaluate linkages between energetic condition and population abundance during and after a recent collapse. We show that abundance declines during the collapse were associated with dramatic declines in energetic condition, and the negative impact of high population density on energetic reserves was intensified by warming during a marine heatwave. Elevated energetic condition coincided with strong recruitment post-collapse, suggesting rapid initial population recovery in the eastern Bering Sea. However, we show that cold-water habitat (≤ 0°C) is critical for supporting high snow crab density in rebuilding towards a pre-collapse state. These results suggest that warming and loss of sea ice will exacerbate the risk of collapse in snow crab through energetic constraints on survival. Furthermore, we highlight the validation of an indirect energetic condition metric that will facilitate continued energetics monitoring and rapid integration into management.

Key words: Bering Sea, Chionoecetes opilio, energetics, fatty acids, marine heatwave, population collapse

INTRODUCTION

Climate change is rapidly increasing thermal risk for populations, and mass mortality events related to marine heatwaves are increasingly common, most notably for invertebrates (Fey et al. 2015). Discrete and prolonged periods of anomalously warm water that define marine heatwaves have increased in frequency, duration and spatial extent during the past decade in northern latitudes such as the Bering Sea (Hobday et al. 2016; Carvalho et al. 2021). Snow crab (*Chionoecetes opilio*), in particular, are highly vulnerable to marine heatwaves, as they are highly stenothermic and rely on cold bottom waters associated with seasonally ice-covered habitats. Recent and rapid sea ice loss in the Bering Sea have exacerbated the loss of these cold-water habitats, and predictions of ice-free conditions in coming decades raise concern for ice-associated species (Wang and Overland 2012; Notz and Stroeve 2016; Overland and Wang 2025). During 2018-2019, a marine heatwave in the Bering Sea resulted in the lowest winter sea ice extent on record and extreme bottom water warming (Stabeno and Bell, 2019). The snow crab population in the eastern Bering Sea abruptly collapsed following the marine heatwave, declining from the highest-observed abundance in 2018 to the lowest-observed in 2021 (Szuwalski et al. 2023). The highly valuable fishery for Bering Sea snow crab was subsequently closed for the first time in history during the 2022-2023 and 2023-2024 seasons.

Considered one of the largest mass mortality events of motile marine macrofauna in recent history, the snow crab collapse was attributed to the 2018-2019 marine heatwave and unprecedented sea ice loss (Szuwalski et al. 2023; Litzow et al. 2024). In particular, elevated snow crab mortality during the collapse was linked to high population density and a temperature-driven increase in metabolic demand, suggesting that starvation was the proximate cause for the collapse. However, these conclusions concerning the role of starvation were drawn, in part, from reductions in snow crab body weight-at-size (Szuwalski et al. 2023), despite evidence that morphological indices of condition are highly insensitive in detecting energy depletion and starvation-induced mortality in snow crab (Hardy et al. 2000; Lorentzen et al. 2020; Kruse 2023). Biochemical indices (e.g., lipid and fatty acid content) provide direct estimates of energetic condition (Copeman et al. 2018; Copeman et al. 2021) and, as such, are better suited to evaluate energetic constraints and bottom-up food limitation (Stevenson and Woods 2006). Energetic status can have a strong effect on starvation and mortality risk, and declines in population abundance are often closely linked to reduced energetic condition (Dutil and Lambert 2000). Likewise, energetic metrics

(Mullowney and Rose 2014; Receveur et al. 2022), while rebounding energetic condition can reflect population recovery. Despite the potential for energetic condition indices to improve our understanding of population fluctuations and to provide early detection of impending mortality events, energetic condition is not routinely monitored in Bering Sea snow crab. This paucity of data is, in part, due to the absence of practical condition metrics that 1) have been validated against more sensitive biochemical indices, and 2) can be rapidly measured and analyzed in time to directly inform fisheries management decisions each fall.

Patterns of variability in energetic condition are often reflective of environmental conditions, food quantity and quality, and density dependence. While reductions in sea ice cover and warming in the Bering Sea are predicted to alter benthic-pelagic coupling and reduce energy available to benthic communities (Overland and Stabeno 2004; Grebmeier et al. 2006; Lovvorn et al. 2016), our understanding of snow crab prey availability remains limited. Declines in juvenile snow crab body condition have been associated with warmer temperatures and declines in ice-associated diatom production in the Bering Sea, suggesting that temperature is an indirect driver of shifts in prey quality (Copeman et al. 2021). Likewise, evidence for climate-driven range contractions in snow crab points towards potential reductions in foraging area and prey availability as outcomes of warming (Fedewa et al. 2020; Szuwalski et al. 2023). Because population collapses can alter responses to environmental drivers (Durant et al. 2024), energetic responses to warming and record-high population density preceding the snow crab collapse may fundamentally differ from post-collapse responses when abundances are low. Elucidating the magnitude, direction and potential interactions between population density and temperature effects is critical in identifying drivers of collapse risk in the Bering Sea snow crab population.

To date, efforts to understand the snow crab collapse have solely focused on the eastern Bering Sea portion of the population despite support for high connectivity with snow crab in the northern Bering Sea (Ernst et al. 2005; Parada et al. 2010 Juvenile snow crab occupy a latitudinal gradient in the Bering Sea, with high densities extending northward into more consistently ice-covered areas of the northern

Bering Sea (north of ~60°N). The southern extent of their range is limited to shallow, cold-water habitats in the eastern Bering Sea (Murphy et al. 2010). While the largest magnitude of decline during the snow crab collapse occurred in juvenile nursery grounds in the eastern Bering Sea , the northern Bering Sea population also experienced declines in abundance coinciding with the 2018-2019 marine heatwave (Fedewa et al. 2020). However, sea ice loss and population declines in the north were less pronounced than in the eastern Bering Sea. This latitudinal population gradient and contrast in vulnerability to collapse provide a novel opportunity to compare energetic responses to population density and warming in collapsing and non-collapsing portions of the juvenile snow crab population during a marine heatwave.

The north-south latitudinal gradient in juvenile snow crab habitat and seasonal ice coverage also offers an opportunity to define optimal thermal habitat for snow crab by evaluating regional differences in energetic status across the full spatial extent of the Bering Sea. Anticipating the impacts of warming on thermal habitat suitability necessitates a better understanding of temperature effects on direct drivers of mortality risk such as energetic state. Bottom temperature appears to be an important predictor of snow crab habitat in the Bering Sea, and maximum thermal thresholds for snow crab have traditionally been defined as 2°C (Mueter and Litzow 2008; Murphy 2020). However, realized thermal niches likely differ in more consistently seasonally ice-covered habitat in the northern Bering Sea, and lower thermal preferences proposed for ice-associated species suggest that 1°C may be more biologically meaningful in delineating optimal thermal habitat for snow crab (Kotwicki and Lauth 2013). Furthermore, ecological insight into snow crab thermal preferences is critical for defining suitable habitat for population rebuilding, and predicting climate-mediated changes in habitat use and availability.

Here, we evaluate the role of energetics in collapse and recovery potential using a direct measure of energetic condition (i.e., total fatty acids in the hepatopancreas) applied across the collapsing (eastern) and non-collapsing (northern) portions of the Bering Sea snow crab population. Our specific objectives are to 1) test the hypothesis that energetic condition of juvenile snow crab covaries with population abundance during and after the collapse in the two regions; 2) test for regional differences in the interactive effect of snow crab density and temperature on energetic condition; 3) use energetic condition to test for thermal optima that define suitable habitat for population recovery; and 4) evaluate an indirect condition metric (i.e., hepatopancreas percent dry weight) to allow routine rapid monitoring of energetic condition for early detection of future population declines. Ultimately, our approach will shed light on the causes and consequences of a mortality event underlying one of the largest marine invertebrate population collapses in recent history, and facilitate a better understanding of population recovery potential.

MATERIALS AND METHODS

Study site and study population

We collected hepatopancreas samples from juvenile snow crab (i.e., immature, pre-terminal molt individuals) across a latitudinal gradient on Alaska Fisheries Science Center Bering Sea bottom trawl surveys to allow for comparison of energetic condition in the northern and eastern portions of the Bering Sea continental shelf within the U.S. Exclusive Economic Zone. These two regions of the Bering Sea are targeted by separate bottom trawl surveys (annual in the eastern Bering Sea, biennial in the northern Bering Sea), and the fishery occurs exclusively in the eastern Bering Sea. Furthermore, these two portions of the snow crab population experienced different population trajectories following the extreme low-ice years of 2018-2019. Estimated snow crab abundance in the eastern Bering Sea reached a time series high in 2018 but declined more than 92% by 2021 (Fig. 1a). Abundance in the northern Bering Sea reached a similar high point in 2017 and declined 60% by 2021. In addition to the smaller proportional decline in the northern Bering Sea, this portion of the population showed a more rapid recovery, with abundance in 2022-2023 reaching 48-60% of the 2017 high point, while abundance in the eastern Bering Sea remained depressed until 2024 (Fig. 1a).

Sampling design and data collection

We sampled juvenile snow crab during the 2019 and 2021-2024 eastern Bering Sea bottom trawl surveys, and the 2019 and 2021-2023 northern Bering Sea bottom trawl surveys. The northern Bering Sea trawl survey was not conducted in 2024 following its transition to a biennial survey, and neither survey was conducted in 2020 due to the COVID-19 pandemic. The eastern Bering Sea bottom trawl survey occurs annually during May-July, with sampling conducted across 375 stations. The northern Bering Sea bottom trawl survey encompasses an additional 144 standardized stations that are sampled in August. Surveys in both regions utilize a systematic design (20 × 20 nautical mile grid) and an 83-112 Eastern bottom trawl (Stauffer 2004).

To ensure representative spatial coverage for energetics sampling in the two regions, we defined eight strata within the eastern and northern survey grids for stratified random sampling of juvenile snow crab habitat encompassing the middle and outer shelf of the Bering Sea. Stratum boundaries were delineated using marine regions developed by Ortiz et al. (2013), which are characterized by distinct ecological domains and oceanographic and bathymetric features. In each study year, we collected juvenile snow crab at a minimum of five survey stations within each stratum, aiming for a collection goal of 20 male and 20 female snow crab per stratum (Table 1). We limited our collections to juvenile snow crab because energetic constraints on survival may be significantly more pronounced in juveniles as they undergo energetically costly molting events. Furthermore, baseline levels of total lipids and fatty acids vary with ontogeny and molt stage (Copeman et al. 2012), so we minimized potential age-based or ontological variability in our samples by employing minimum carapace width size thresholds to target pseudo-cohorts of newshell immature snow crab in the eastern Bering Sea (≥ 70 mm carapace width males, ≥ 45 mm carapace width females) and the northern Bering Sea (≥ 50 mm carapace width males, ≥ 40 mm carapace width females). The size classes we targeted in the eastern Bering Sea portion of the population are expected to molt to maturity the following spring. Slightly smaller pseudo-cohorts were collected in the northern Bering Sea portion of the population because large immature snow crab are encountered infrequently in this region due to smaller size at maturity (Divine et al. 2019) and directional northeast to southwest ontogenetic migrations (Ernst et al. 2005, Parada et al. 2010). Morphometric maturity in female snow crab was determined visually by assessing abdomen flap morphology (Jadamec et al. 1999). Male maturity was estimated with a distribution-based cutline approach that utilizes an allometric relationship between chela height and carapace width (Richar and Foy 2022). Specimen collections were conducted under permits from the Alaska Department of Fish and Game (permit numbers CF-19-032BT and CF-22-022BT).

Modeling Covariates

We estimated snow crab density at each station sampled by dividing the total number of all snow crab caught by area-swept effort (catch per unit effort; crab/nm^2). Density estimates were right-skewed, so we fourth-root transformed CPUE data prior to use in statistical models to improve model fits. To compare snow crab population abundance trajectories in each region (Fig. 1a), we multiplied average snow crab density estimates across all survey stations within the respective eastern and northern Bering Sea survey grids by the survey grid area for each region. While our calculated abundance estimates do not implicitly account for poor survey gear selectivity of snow crab < 40 mm carapace width (Somerton et al. 2013), abundance estimates are assumed to be a consistent measure of population size because selectivity is unlikely to have changed during our study period.

We measured bottom temperature at each station using a Sea-Bird SBE-39 datalogger (Sea-Bird Electronics Inc., Bellevue, WA) attached to the trawl headrope. Because summer bottom temperatures in the Bering Sea are significantly influenced by the maximum extent of spring sea ice, the timing of its retreat, and the formation of a cold, dense bottom-water layer (Stabeno et al. 2012), we also compared the magnitude of sea ice loss in the eastern and northern Bering Sea to characterize region-specific impacts of the 2018-2019 marine heatwave relative to our summer sampling efforts and estimates of energetic condition. To quantify sea ice loss, we plotted the spatial extent of average March sea ice concentration ≥

15% using data from the ERA5 global reanalysis (Dee et al. 2011). This regional sea ice extent comparison shows that the eastern Bering Sea experienced a near-complete loss of sea ice in spring 2019, followed by the return of sea ice in 2021-2024, whereas the northern Bering Sea received at least partial ice coverage each spring (Fig. 1b).

Energetic analyses

Because the hepatopancreas is the primary energy storage organ in crustaceans, we collected hepatopancreas samples at sea for fatty acid analyses used to measure snow crab energetic condition. Snow crab were dissected on the survey vessel by opening the carapace and removing approximately 1g of hepatopancreas tissue from the body cavity, above the heart and gonads. Hepatopancreas samples were frozen at -40°C in sealed Eppendorf tubes wrapped in Teflon tape for three to six months prior to processing. To measure hepatopancreas percent dry weight (i.e. indirect energetic condition metric), samples were briefly thawed and rigorously mixed to a homogeneous consistency.

(± 0.001 g)

pre-weighed aluminum tray, drying at 65 °C for 72 hours to a constant mass, and then weighing to determine the dry weight (DWT, g).

To measure total fatty acid concentration (i.e. direct energetic condition metric), we used a 100 mg sample of wet hepatopancreas. Tissues were weighed (approx. 100 ± 0.001 mg) into lipid-cleaned 15 mL thick-walled glass tubes with Teflon-lined screw caps. An internal standard (23:0 methyl ester) was added at 10% of the estimated total fatty acid weight. We dried internal standards and hepatopancreas tissues under a steady stream of nitrogen gas until all visible moisture was removed from the sample. Fatty acid methyl esters (FAME) were synthesized using a rapid one-step acid-catalyzed direct extraction and methylation procedure. Following Meier et al. (2006), 1 ml of anhydrous methanol containing 2.5M HCl was added to tissue samples and derivatized. Select samples were checked to assure complete derivatization of lipids to FAMEs using thin-layer chromatography with flame ionization detection (TLC_FID) on a Mark VI Iatroscan (Copeman et al. 2021). Quantitative FAME measures were determined using gas chromatography with flame ionization detection (GC- FID) on a HP 7890 GC-FID equipped with an autosampler and a DB wax + GC column (Agilent Technologies, Inc., U.S.A.). The column was 30 m in length, the internal diameter was 0.25 mm and the column film thickness was 0.25 µm. The oven temperature began at 65°C and was held at this temperature for 0.5 min. Oven temperature was increased to 195°C (40°C/min), held for 15 min then increased again (2 °C/min) to a final temperature of 220°C, which was held for 1 min. The hydrogen carrier gas flowed at a rate of 2 ml/min and the injector and detector temperatures were set at 250°C. Peaks were identified using retention times based upon standards purchased from Supelco (37 component FAME, BAME, PUFA 1, PUFA 3). Chromatograms were integrated using Chem Station (version A.01.02, Agilent). Total fatty acid concentration in the hepatopancreas was expressed as either total fatty acids (mg) per wet weight (WWT, g) or dry weight (DWT, g).

Data analyses

Objective 1: Covariation between energetic condition and snow crab abundance. To evaluate evidence for regional variation in energetic condition during and after the snow crab collapse, we used Bayesian hierarchical regression models to generate annual estimates of mean energetic condition and 95% credible intervals for the collapsing (eastern) and non-collapsing (northern) portions of the population. We began by estimating annual mean energetic condition and uncertainty for each region to compare time series of energetic status for the two portions of the population. These estimates were generated using separate models for each region, since we were not interested in sharing information across regions. The model for each region took the form:

$$Y_{t,i,j,s} = \beta_0 + \beta_1 YEAR_t + f_1\,(SIZE_s) + \ f_2\,(DOY_{t,i}) + \ \alpha STRATUM_j + \varepsilon_{t,i,j,s} \qquad (1)$$

where $Y_{t,i,j,s}$ is the total fatty acids per wet weight estimate for a snow crab sampled in year t at station i in stratum j at size s, β_0 is the intercept, YEAR is a categorical population-level (fixed) effect, f_1 is a smooth function of crab carapace width (SIZE), f_2 is a smooth function of the Julian day at which station i was sampled in year t (day of year, DOY), α_j is a group-level (random) effect to account for spatial autocorrelation of samples collected within sampling stratum j, and $\varepsilon_{t,i,j,s}$ is the individual-level residual error. We included snow crab carapace width and sampling day as control variables to account for potentially confounding influences of seasonality and ontogeny on our energetic condition estimates. Non-linear relationships were accounted for in the effect of continuous variables (i.e., crab size and sampling day) using thin plate regression splines, and smooths were limited to three basis functions to avoid overfitting. Models utilized a zero-truncated Gaussian response distribution and flat priors.

Next, we used these model-derived annual estimates of energetic condition to support a comparative analysis between energetic condition and population change to assess whether stronger and more persistent declines in abundance in the collapsing eastern Bering Sea covaried with declines in energetic condition. Our study design provides a dataset spanning five years and two regions, which we judged as too small to support a robust regression-based analysis of region-specific energetic condition at an annual scale. Accordingly, we used the annual energetic condition estimates produced from region-specific regression models (Eq. 1) and compared these to eastern and northern Bering Sea snow crab population-level abundance estimates derived from the full survey grid for each respective region (Fig. 1a) to qualitatively assess for covariation (i.e., synchronous changes in the direction of abundance and energetic condition estimates).

Objective 2: Interactive effects of population density and temperature. To evaluate evidence for an interactive effect of population density and bottom temperature on energetic condition, and to test whether the strength and direction of this interaction differed between the collapsing and non-collapsing portions of the snow crab population, we fit a single Bering Sea-wide Bayesian regression model that pooled energetic condition estimates across both regions. The full model took the form:

$$Y_{t,i,j,s} = \beta_0 + \beta_1(CPUE_{t,i}, TEMP_{t,i}, REGION) + f_1(SIZE_s) + f_2(DOY_{t,i}) + \alpha STRATUM_j + \varepsilon_{t,i,j,s} \quad (2)$$

where $Y_{t,i,j,s}$ is the total fatty acids per wet weight estimate for a snow crab sampled in year *t* at station *i* in stratum *j* at size *s*, β_0 is the intercept, CPUE is the population-level snow crab density at station *i* sampled in year *t* that interacts with bottom temperature at station *i* sampled in year *t* (TEMP) and the Bering Sea region (REGION), f_1 is a smooth function of crab carapace width (SIZE), f_2 is a smooth function of the Julian day at which station *i* was sampled in year *t* (day of year, DOY), α_j is a group-level (random) effect to account for spatial autocorrelation of samples collected within sampling stratum *j*, and $\varepsilon_{t,i,j,s}$ is the individual-level residual error. The full model was fit using a zero-truncated Gaussian response distribution and flat priors, and smooths were limited to three basis functions to avoid overfitting. We evaluated model performance and out-of-sample predictive skill with the Bayes R^2 (Gelman et al. 2019).

Objective 3: Defining optimal thermal habitat. If there was support for an interaction between temperature and density, we used the Bering Sea-wide regression model (Eq. 2) to evaluate the effect of density dependence on energetic condition at a representative range of temperatures. We *a priori* defined four representative bottom temperature values (0°, 1°, 2°, and 3°C) based on previous research, and evaluated the conditional effects of the density × temperature interaction on energetic condition of collapsing and non-collapsing portions of the population at these four temperature values. This approach enabled us to determine the relative energetic consequences of changes in density and temperature, and to define thermal habitat optima that may promote population recovery.

Objective 4. Evaluating an indirect condition metric. To assess the predictive accuracy of hepatopancreas percent dry weight as a rapid, indirect metric to monitor energetic condition, we used a Bayesian regression model to evaluate the relationship between hepatopancreas percent dry weight and hepatopancreas total fatty acid concentration per dry weight of individual snow crab samples with paired measurements. For this analysis, we fit data from 2021 to 2024 at-sea collections, pooling eastern and northern Bering Sea samples (n = 974). The regression model was fit using a Gaussian response distribution and flat priors.

All Bayesian analyses were conducted in the Stan computational framework (Stan Development Team 2024) and implemented in the 'brms' package (Bürkner et al. 2017) in R v4.4.2 (R Core Team

We conducted estimation with four parallel MCMC chains and 10,000 iterations. Chain convergence and model fits were examined using the potential scale reduction factor ($\hat{R} < 1.05$), effective sample sizes, Leave One Out Probability Integral Transform (LOO-PIT) plots, simulated DHARMa residual plots (Hartig and Hartig 2017) and posterior predictive checks (Gabry et al. 2019; Gelman et al. 2020). We also investigated the sensitivity of the posterior to perturbations of the prior and likelihood to diagnose any prior-data conflicts (Kallioinen et al. 2023). osterior summaries (means and 80/90/95% credible intervals) of conditional effects were estimated to compare energetic condition across collapsing and non-collapsing portions of the population, and ` temperature and density effects on energetic condition.

RESULTS

Overall, a total of 1,325 juvenile snow crab hepatopancreas samples were collected from mid-June to mid-August during the 2019-2024 eastern and northern Bering Sea surveys. Sampled snow crab ranged in size from 40.16 to 113.2 mm carapace width. Over the five-year sampling period, trajectories of snow crab density and bottom temperature at sampled stations differed substantially between the eastern and northern Bering Sea. The collapsing eastern Bering Sea portion of the population showed an 84% decline in mean density from 2019 to 2021 (Fig. 2a). In contrast, density in the non-collapsing northern Bering Sea portion of the population remained, on average, nearly four times higher than density in the collapsing portion of the population from 2021 to 2023. However, the eastern Bering Sea portion of the population showed a possible sign of recovery in 2024, with density increasing over 10-fold from 2023 to 2024. Average bottom temperatures in the eastern Bering Sea exceeded 3°C in 2019, while the northern Bering Sea average bottom temperature remained below 1.5°C during the study period (Fig. 2b).

Covariation between energetic condition and population change

The posterior means estimated from our region-specific eastern and northern Bering Sea models indicate substantial interannual variability in energetic condition in the collapsing (eastern) portion of the population, as evidenced by nonoverlapping 95% credible intervals (Fig. 3). Furthermore, changes in energetic condition in the two regions reflected differences in population trajectories between the collapsing and non-collapsing portions of the population. Mid-collapse (2019), eastern Bering Sea snow crab mean energetic condition fell to 51 mg FA/g WWT (95% credible interval [CI] = 36-73 mg fatty acid /g WWT), a 49-63% decrease relative to posterior means in years following the collapse (101-139 mg fatty acid/g WWT; Fig. 3). Furthermore, a post-collapse increase in energetic condition coincided with substantial increases in eastern Bering Sea snow crab abundance from 2021 to 2024. In contrast, annual estimates of energetic condition were more constant in the non-collapsing northern portion of the population, and mean energetic condition never fell below 80 mg fatty acid/g WWT during the study period (Fig. 3).

Interactive effects of population density and temperature.

The Bering Sea-wide model showed clear support for interactive effects of population density and temperature that differed between the collapsing and non-collapsing portions of the population (density x temperature x region interaction estimate = 1.44, 95% CI = [0.60, 2.29]). Specifically, we found strong support for a negative interaction between temperature and population density on energetic condition in the collapsing portion of the population. Plots of posterior density effects for the collapsing region at four representative temperatures (0°, 1°, 2°, and 3°C) showed negative effects of snow crab density at warmer temperatures (1°C-3°C) and a neutral effect of snow crab density at 0°C (Fig. 4a). In contrast, we did not find support for an interactive effect of temperature and population density on energetic condition in the non-collapsing portion of the population. Instead, posterior density effects at all four temperature levels for the non-collapsing region could not be distinguished from a zero-slope line, and energetic condition remained stable at high densities and high temperatures (Fig. 4b). We also observed a seasonal increase in energetic condition from mid-June to early August (Fig. S1a), and found no evidence for a crab size effect (i.e., the effect could not be distinguished from a zero-slope line; Fig. S1b). The Bering Sea-wide model for energetic condition across collapsing and non-collapsing portions of the snow crab population returned a Bayesian $R^2 = 0.17$. This relatively low proportion of variance explained is likely due to the inclusion of northern Bering Sea data that showed weak responses to model covariates, whereas a reduced version of the model fit only to eastern Bering Sea samples explained roughly a quarter of variance (Bayesian $R^2 = 0.24$).

Performance of a rapid condition metric

We found that the proposed rapid metric was a good predictor of energetic condition, supported by a strong positive relationship between hepatopancreas percent dry weight and total fatty acid concentration (mg/g DWT) across the four years of data (Fig. 5). Percent dry weight of the hepatopancreas explained 64% of the variation in hepatopancreas total fatty acids. The strength of this relationship was consistent among sampling years and regions, indicating strong predictive ability of hepatopancreas percent dry weight as an indicator of energetic reserves in juvenile snow crab.

DISCUSSION

Population collapses are often associated with low rates of recovery (Hutchings and Reynolds 2004), highlighting the need for improved understanding of factors associated with persistent population decline and recovery potential. Here, we used a direct measure of energetic condition in juvenile snow crab to demonstrate empirical linkages between energetic reserves and collapse and population recovery trajectories. Synchronous declines in energetic condition and abundance in the collapsing portion of the Bering Sea snow crab population point to energetic limitations during a marine heatwave as a proximate mechanism for increased mortality and population collapse. While our study adds to the growing evidence linking poor energetic condition to marine population collapses (e.g. Dutil and Lambert 2000;

Sherwood et al. 2007; Barbeaux et al. 2020), our results provide novel insights into collapse risk and vulnerability to warming. We demonstrate that the non-collapsing, northern portion of the snow crab population maintained relatively stable energetic condition associated with a reduced magnitude of warming during the 2018-2019 marine heatwave relative to the eastern Bering Sea. We also show that energetic condition rebounded rapidly in the eastern Bering Sea portion of the population following the collapse and marine heatwave. This finding, coinciding with strong recruitment and increasing population abundance from 2021 to 2024 in the eastern Bering Sea (Fig. 1a), demonstrates support for initial population recovery post-collapse. Likewise, suggests that the snow crab collapse may be reversible when the ecosystem returns to pre-heatwave conditions. While initial recovery appears to be relatively rapid compared to collapses in other species (Hutchings 2000; Neubauer et al. 2013), our results emphasize that successful recruitment to the fishable portion of the snow crab population is critically dependent on conditions that promote increased energetic condition and survival of juveniles. Our study is the first to provide critical perspectives on region-specific energetic outcomes through the inclusion of the non-collapsing portion of the snow crab population, and our results highlight how this comparative approach can improve our understanding of collapse and recovery dynamics.

We attributed declines in energetic condition in the collapsing portion of the population to a strong negative interaction between elevated bottom temperatures and high population density, and we found that temperature mediates the direction and magnitude of density-dependent effects on energetic condition. The ecological interaction detected in our study underscores the energetic consequences associated with the combination of high snow crab density and bottom temperatures ≥ 1°C. We also show that cold-water habitat (≤ 0°C) in the eastern Bering Sea is critical for sustaining high snow crab densities consistent with rebuilding and population recovery. This result is supported by the understanding that snow crab are highly stenothermic and critically reliant on cold temperatures (Dionne et al. 2003). However, our results highlight that an additive interpretation of temperature and density effects on snow crab is inappropriate, as the strength of density-dependent processes was highly influenced by bottom temperature and the effect may, instead, be synergistic. While high population density and unusually warm bottom temperatures have previously been linked to the eastern Bering Sea snow crab collapse (Szuwalski et al. 2023), our approach revealed that energetic responses to density and temperature effects differed regionally between collapsing and non-collapsing portions of the snow crab population. We found no support for interactive effects on energetic condition in the non-collapsing portion of the population to the north, where our results suggest that juvenile snow crab are able to maintain energetic reserves across the full range of temperatures and population densities observed in the northern Bering Sea during our study period. Strong benthic-pelagic coupling and carbon flux to the benthos have historically supported high macrofaunal biomass in the northern Bering Sea (Grebmeier et al. 1988), suggesting that ample benthic prey resources may buffer juvenile snow crab from potential declines in energetic condition despite increased metabolic demand at higher temperatures. Conversely, high population densities and extreme temperatures in the collapsing portion of the population may require snow crab to utilize energetic reserves to offset density-dependent reductions in prey availability and thermally-driven increases in metabolic rates. However, we caution that our conclusion supporting interactive density and temperature effects is based on a limited set of observations in our study period. In particular, energetic responses have not yet been observed under a combination of high temperatures and low densities in the collapsing portion of the population.

Past studies have defined snow crab thermal habitat preferences in the Bering Sea using presence/absence or abundance data derived from fishery-independent surveys (Murphy 2020; Fedewa et al. 2020), although these approaches lack causal mechanisms. We improve on this limitation by utilizing energetic condition as a proximate mechanism for survival to demonstrate that temperatures ≤ 0°C are more meaningful in defining optimal thermal habitat for high-density juvenile snow crab nurseries than previously-defined 2-3°C Bering Sea thresholds (Litzow and Mueter 2008; Murphy 2020). Similarly, the cold intermediate layer (CIL) in Atlantic Canada, defined as waters below 0°C, is closely associated with snow crab spatial distributions and habitat (Dionne et al. 2003), lending support to our findings. However, this 0°C temperature optimum appears to be biologically meaningful to the collapsing portion of the snow crab population only, and we found evidence for a larger realized thermal niche in the non-collapsing portion of the population. While laboratory studies indicate that thermal tolerances were likely not exceeded during the 2018-2019 marine heatwave (Foyle 1989), laboratory conditions often poorly predict realized thermal niches. Our study, instead, highlights the importance of conspecific density, availability of bottom waters ≤ 0°C, and energetic status when defining thermal preferences for Bering Sea snow crab.

Despite the strengths of our approach, a direct mechanism for regionally-varying thermal responses observed in this study remains unclear. Declines in eastern Bering Sea snow crab abundance during the marine heatwave were driven by a broader ecosystem transition from Arctic to boreal conditions, and an index of this ecosystem reorganization outperformed bottom temperatures alone as a predictor of declining snow crab abundance (Litzow et al. 2024). This result, combined with illustrated linkages between snow crab productivity and both sea ice extent and large-scale climate indices (Szuwalski et al. 2020; Mullowney et al. 2023), suggest that invoking temperature as a mechanistic driver for shifts in energetic condition likely oversimplifies complex ecosystem responses linked to spring sea ice dynamics and food availability to the benthos (Copeman et al. 2025). Given that the northern Bering Sea has not yet reached environmental extremes evidenced in the eastern Bering Sea in recent decades (Stabeno and Bell 2019; Overland et al. 2024) and spring sea ice covered the majority of snow crab habitat in the northern Bering Sea during the marine heatwave (Fig. 1b), we propose that the presence of spring sea ice may mediate the negative consequences of elevated temperatures and high population density that impacted the collapsing portion of the population to the south. This idea is further supported by findings that minimum sea ice extent thresholds drive shifts in the northern Bering Sea zooplankton community (Kimmel et al. 2023) and the prevalence of open-water spring phytoplankton blooms (Nielsen et al. 2024), which collectively influence the availability of basal resources to the benthos. Taken together, these results emphasize that continued warming and loss of sea ice in the northern Bering Sea may reveal temperature thresholds and critical tipping points in the non-collapsing portion of the population as this system continues to encounter conditions that are outside the envelope of historic observations.

Rapid warming in the Bering Sea poses a pressing challenge to fisheries management, and decision makers are increasingly reliant on real-time indicators of ecosystem and population conditions to capture shifts in stock productivity (Caddy 2004). Here, we present a rapid indirect measure of energetic condition (i.e., percent dry weight of the hepatopancreas) that effectively tracks bottom-up effects on snow crab productivity, and accurately predicts direct biochemical energetic condition measurements that are highly sensitive to environmental change in the Bering Sea. Our results also highlight the utility of a rapid energetic condition metric that effectively replaces time-intensive and cost-prohibitive biochemical analyses that can delay the uptake of energetics data. While percent dry weight of the hepatopancreas has previously been utilized to estimate energetic condition in laboratory-reared snow crab (Hardy et al. 2000; Godbout et al. 2002), we are unaware of any efforts to date that have employed this metric annually to provide a rapid health assessment for monitoring snow crab populations. Co-varying energetic condition and population abundance trajectories in this study suggest that our validated rapid energetic condition metric can provide inference about likely population trends, thus providing strong support for operational use in fisheries management. The recent development and integration of stock-specific Ecosystem and Socioeconomic Profiles (Shotwell et al. 2023) and risk tables (Dorn and Zador 2020) into the North Pacific Fishery Management Council decision-making process provides a mechanism for direct integration of our rapid condition metric into Bering Sea crab management decisions, and supports approaches to ecosystem-based fisheries management (Kruse et al. 2025).

Our work highlights the importance of continued field collections and energetic-based monitoring to facilitate a more robust exploration of mechanistic relationships between energetics, sea ice dynamics, and population outcomes, which are critical to developing skillful forecasts of collapse potential and climate change impacts. While we consider our energetics dataset to be highly effective in tracking population trajectories in Bering Sea snow crab, our results are inherently limited in scope due to our short observation period (five years). Our models explained a fairly low amount of variation in energetic condition estimates, suggesting that future efforts should focus on elucidating direct drivers of energetic condition such as prey quantity and quality. Furthermore, while there is strong evidence that depleted hepatopancreas lipid stores are indicative of starvation-induced mortality in snow crab (Hardy et al. 2000), groundtruthing our field-collected measures of energetic condition with demographic outcomes in laboratory experiments is a necessary next step to determine critical energetic thresholds and physiological tipping points for survival (Lambert and Dutil 1997; Dutil and Lambert 2000). Such applications would facilitate the development of operational, condition-corrected natural mortality rates for direct incorporation into stock assessments (Casini et al. 2016; Regular et al. 2022; Björnsson et al. 2022), or provide a mechanistic basis for time-varying natural mortality estimates (Szuwalski 2022). Despite these limitations, our findings highlight important advances in the understanding of collapse and recovery dynamics, and we anticipate that our empirical approach and development of a rapid energetic condition metric will improve the ability to detect impending population collapses.

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Table 1. Sample sizes for hepatopancreas collections from juvenile snow crab to estimate energetic condition in the collapsing eastern Bering Sea and non-collapsing northern Bering Sea portions of the snow crab population.

	2019	2021	2022	2023	2024	Total
Eastern Bering Sea	98	168	138	189	178	771
Northern Bering Sea	126	192	127	109		554
Total	224	360	265	298	178	1325

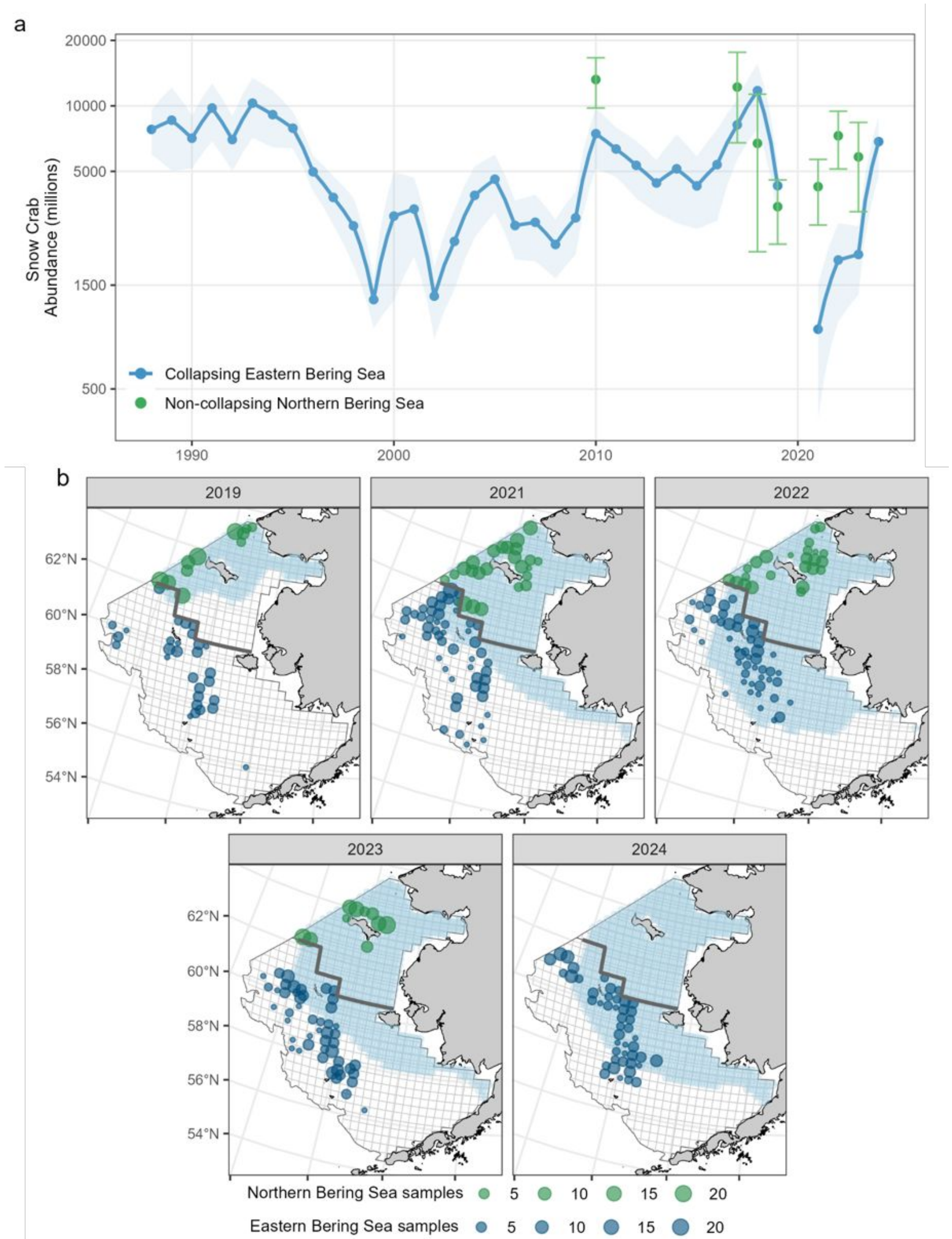

Figure 1. Study system. a) Abundance estimates for the collapsing eastern Bering Sea (blue line ± 95% CI) and non-collapsing northern Bering Sea (green points ± 95% CI) portions of the snow crab population. Note log scale on y-axis. b) Juvenile snow crab hepatopancreas sampling effort on eastern Bering Sea bottom trawl surveys (2019, 2021-2024) and northern Bering Sea bottom trawl surveys (2019, 2021-2023) relative to sea ice cover. Blue shaded areas indicate regions with mean March sea ice concentration ≥ 15%, grid cells indicate standard survey stations, heavy grey line indicates the boundary between the eastern and northern Bering Sea study regions, and green and blue bubbles indicate snow crab sample size by region. Note that the northern Bering Sea was not sampled in 2024. Maps use the Alaska Albers projection and NAD83 datum (Rohan 2024).

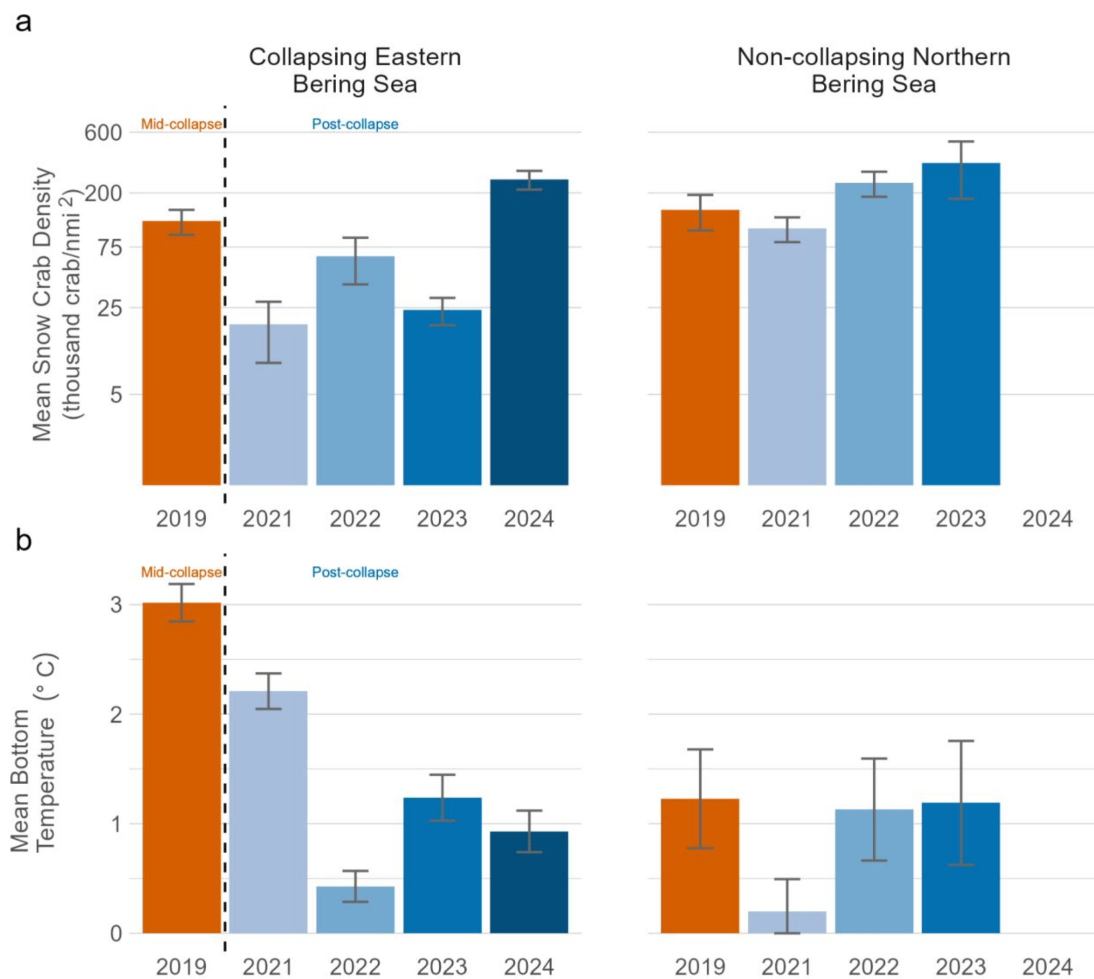

Figure 2. Observed snow crab densities and temperatures coinciding with the eastern Bering Sea population collapse and marine heatwave in 2019. a) Average snow crab population density (± SE) at sampled eastern and northern Bering Sea survey stations during (2019) and after (2021-2024) the eastern Bering Sea population collapse. Note log scale on y-axis. b) Average bottom temperature (± SE) at sampled eastern and northern Bering Sea survey stations. Note that the northern Bering Sea was not sampled in 2024.

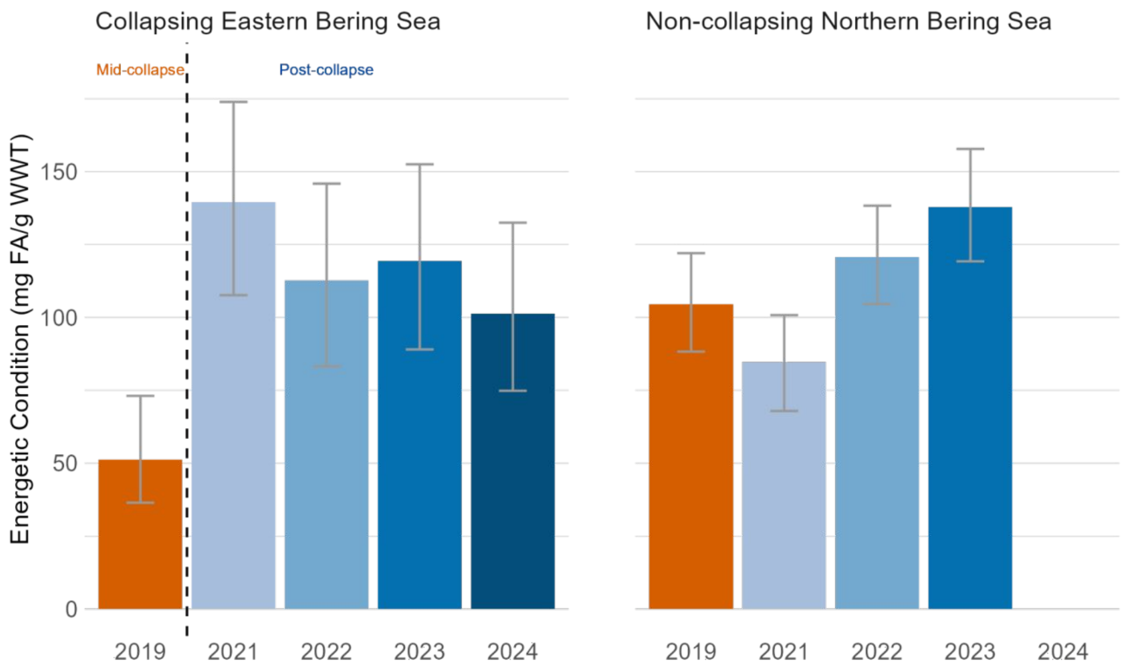

Figure 3. Annual estimates of Bering Sea snow crab energetic condition. Colors designate sampling years during the eastern Bering Sea population collapse (2019) and following the population collapse (2021-2024). Plotted values are posterior means of energetic condition (total fatty acids per wet weight) with 95% credible intervals from a Bayesian regression model controlling for crab size and seasonality.

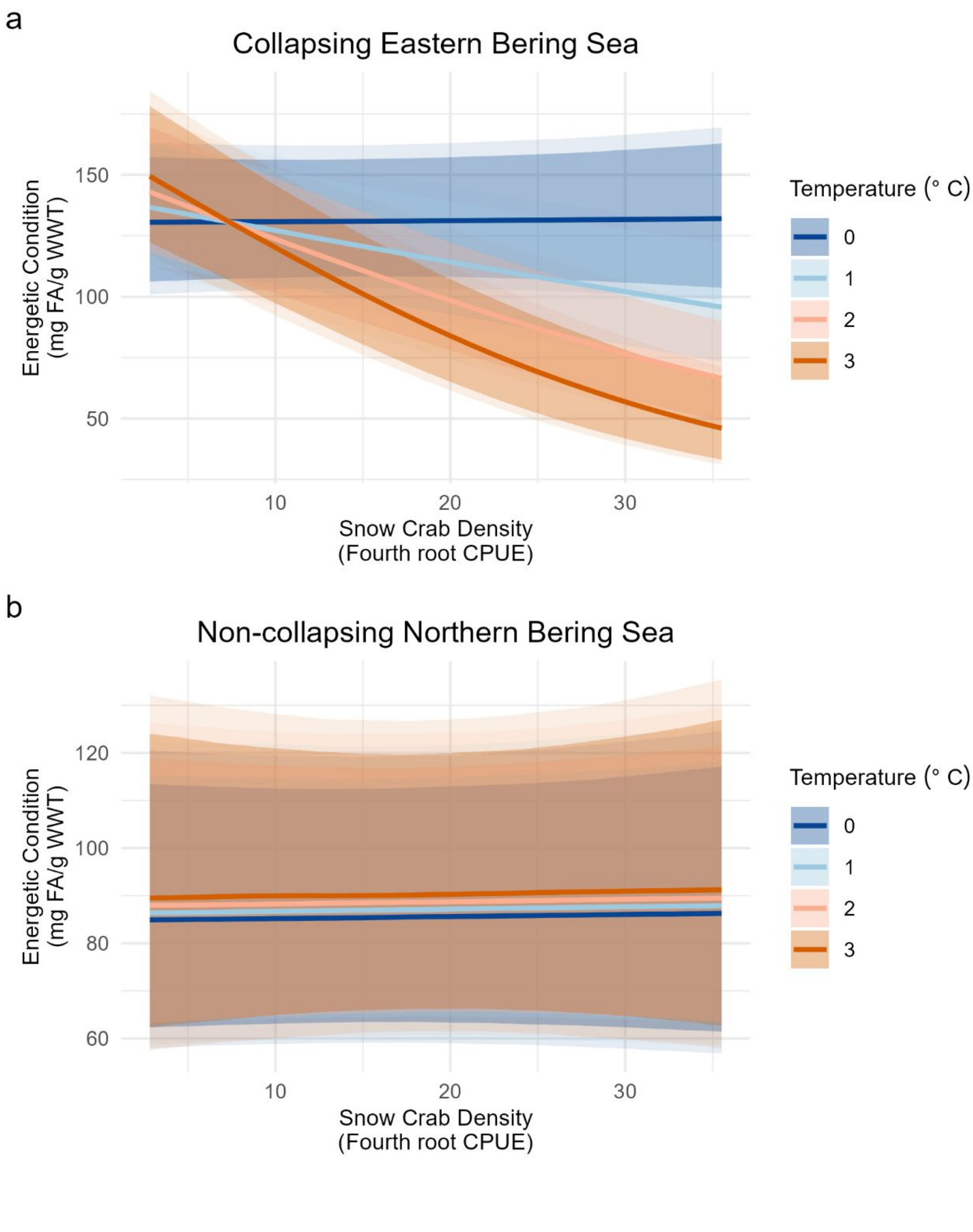

Figure 4. Population density and temperature effects on energetic condition of the collapsing eastern Bering Sea and non-collapsing northern Bering Sea portion of the snow crab population. (a) Predicted conditional effects (posterior means ± 90/95% CIs) of the interaction between snow crab density and bottom temperature on eastern Bering Sea snow crab energetic condition (total fatty acids per wet weight) across all years sampled (2019, 2021-2024); (b) and (c) Predicted conditional effects (posterior means ± 80/90/95% CIs) of the interaction between snow crab density and bottom temperature on northern Bering Sea snow crab energetic condition across all years sampled (2019, 2021-2023).

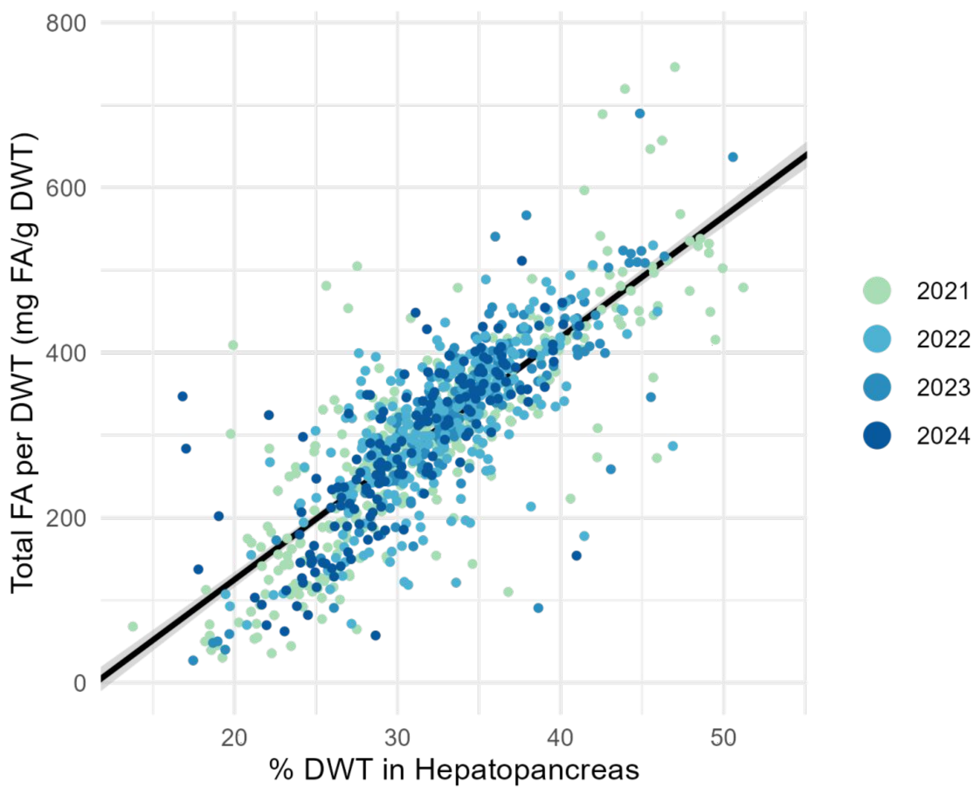

Figure 5. The linear relationship between the percentage dry weight and total fatty acids per dry weight of the hepatopancreas in juvenile snow crab. Plotted values are the predicted relationship and 95% credible intervals from a Bayesian regression model fit to observed data (2021-2024).