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MARINE HEATWAVES

The collapse of eastern Bering Sea snow crab

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The snow crab is an iconic species in the Bering Sea that supports an economically important fishery and undergoes extensive monitoring and management. Since 2018, more than 10 billion snow crab have disappeared from the eastern Bering Sea, and the population collapsed to historical lows in 2021. We link this collapse to a marine heatwave in the eastern Bering Sea during 2018 and 2019. Calculated caloric requirements, reduced spatial distribution, and observed body conditions suggest that starvation played a role in the collapse. The mortality event appears to be one of the largest reported losses of motile marine macrofauna to marine heatwaves globally.

Snow crab (*Chionoecetes opilio*) is one of the most abundant and widely distributed species in the benthic ecosystem of the eastern Bering Sea. The snow crab population has supported an iconic fishery valued at ~US$150 million (ex-vessel average from 2012 to 2021), and fisheries management in Alaska is considered some of the most effective in the world (*1*). A key component of this management is a yearly bottom trawl survey conducted by the National Marine Fisheries Service that monitors the size and number of snow crab on the eastern Bering shelf (Fig. 1A). Many field and laboratory studies aimed at understanding population processes such as growth and maturity have also been performed (*2*). Despite this attention and effort, the stock unexpectedly collapsed in 2021.

The collapse in 2021 occurred 3 years after the observed abundance of snow crab was at historical highs (Fig. 1C). Groups of crab of similar sizes are called "pseudocohorts" because true cohorts cannot be identified as a result of difficulties in aging crab associated with the loss of the hard body parts during the molting process. The largest pseudocohort on record began to be observed in the survey beginning in 2015 and unexpectedly declined by roughly half from 2018 to 2019 (Fig. 1D). The survey was cancelled in 2020 because of the coronavirus pandemic. The 2021 survey found the fewest snow crab on the eastern Bering Sea shelf since the survey began in 1975. More than 10 billion crab disappeared from the eastern Bering Sea shelf from 2018 to 2021 (*3*).

Hypotheses to explain the disappearance fall under two categories: Either the crab are still alive, but the survey did not sample them, or the crab died. It is possible that the crab are in the eastern Bering Sea but were poorly sampled by the most recent surveys. If this were the case, one would expect estimates for other morphometrically similar species such as Tanner crab to have declined unexpectedly, but the population trend for Tanner crab increased (fig. S1). Movement to the northern Bering Sea could account for declines in the eastern Bering Sea, but surveys in the northern Bering Sea did not find crab in the quantities or of the correct sizes to explain declines in the southeast (Fig. 1A). Movement west into Russian waters is another possibility, but Russian scientists reported declines in catch per unit effort in 2020 (*4*), which one might not expect if crab from Alaska emigrated. In addition, it is possible that the crab moved into deeper waters on the Bering Sea slope. The high fishery catch per unit effort in deeper waters during the 2021 fishery supports this possibility to some extent, but the amount of available habitat is <10% of that on the shelf (*5*), and fishery catch per unit effort during 2022 was the lowest on record (fig. S2). Consequently, it is unlikely that all of the missing crab from the shelf are on the slope. Given these observations, mortality is a likely culprit for the bulk of the collapse.

Changes in temperature, predation, fishery effects, disease, and/or cannibalism could affect mortality rates. Snow crab are generally associated with cold water, but they can function in waters up to 12°C in the laboratory (*6*). A marine heatwave occurred in the Bering Sea during 2018 and 2019, and the "cold pool" (a mass of water <2°C on the sea floor with which juvenile snow crab are associated) was absent during this period (Fig. 1B). Although not fatal, the resulting bottom temperatures could affect metabolic rates and alter intra- and interspecific interactions. Smaller crab are a major component in the diet of Pacific cod in the Bering Sea (*7*), and recent changes in the distribution and abundance of cod and crab have contributed to increased consumption of crab by cod (fig. S3). Removals by the snow crab fishery and incidental mortality in fisheries for other species in the Bering Sea may also affect the population dynamics of snow crab. Cannibalism of smaller crab by larger crab is another possible source of mortality and has been suggested as an important driver of population dynamics in eastern Canadian populations (*8*). Last, bitter crab syndrome, a fatal disease that results from infection by a dinoflagellate (*9*), has been observed more frequently in the survey in the past several years and is generally associated with warmer conditions and high densities of immature crab.

To understand the recent collapse, we first attempted to understand the historical variability in mortality. We fitted a population dynamics model to the abundance and size composition data for male crab and estimated recruitment (small crab entering the population) and a maturity- and year-specific total mortality. "Total mortality" represents the fraction of crab dying from any cause in a given year. We then collated maturity-specific time series of potential stressors from 1990 to 2019 and used them in generalized additive models (GAMs) (*10*) to predict total mortality estimated from the population dynamics models (detailed methodology, sensitivities, and simulation testing are provided in the supplementary materials, materials and methods).

The population dynamics model fitted the indices of abundance and size composition data from the survey well, which is not unexpected, given the flexibility of the model (Fig. 2, A and B). Estimated mortality was higher and more varied for mature crab than for immature crab, and estimated mortalities in 2018 and 2019 were the some of the highest in the time series for immature and mature crab. We simulated snow crab populations with time variation in mortality to understand the ability of our population dynamics model to estimate these quantities with the available data. The correlation between estimated mortality and simulated mortality were high, which suggests that analyses relating estimates of mortality and environmental covariates are justifiable (supplementary materials, materials and methods).

GAMs fitted to estimated immature and mature mortality explained ~78 and ~71% of the variability, respectively (Fig. 2C). Higher temperatures and higher densities of mature crab were significantly associated with higher estimated mortality for mature crab. Higher temperatures were also associated with higher immature mortality, but the best-fitting relationship between immature mortality and mature density was dome shaped. The importance of temperature and density was robust to changes in data quantity (such as leave-one-out cross validation), consideration of the uncertainty in mortality estimates, and randomization trials (supplementary materials, materials and methods).

Our results do not support a strong connection between variability in snow crab mortality and indices of trawling, predation, cannibalism, or disease. All of these forces must contribute to underlying mortality to some degree,

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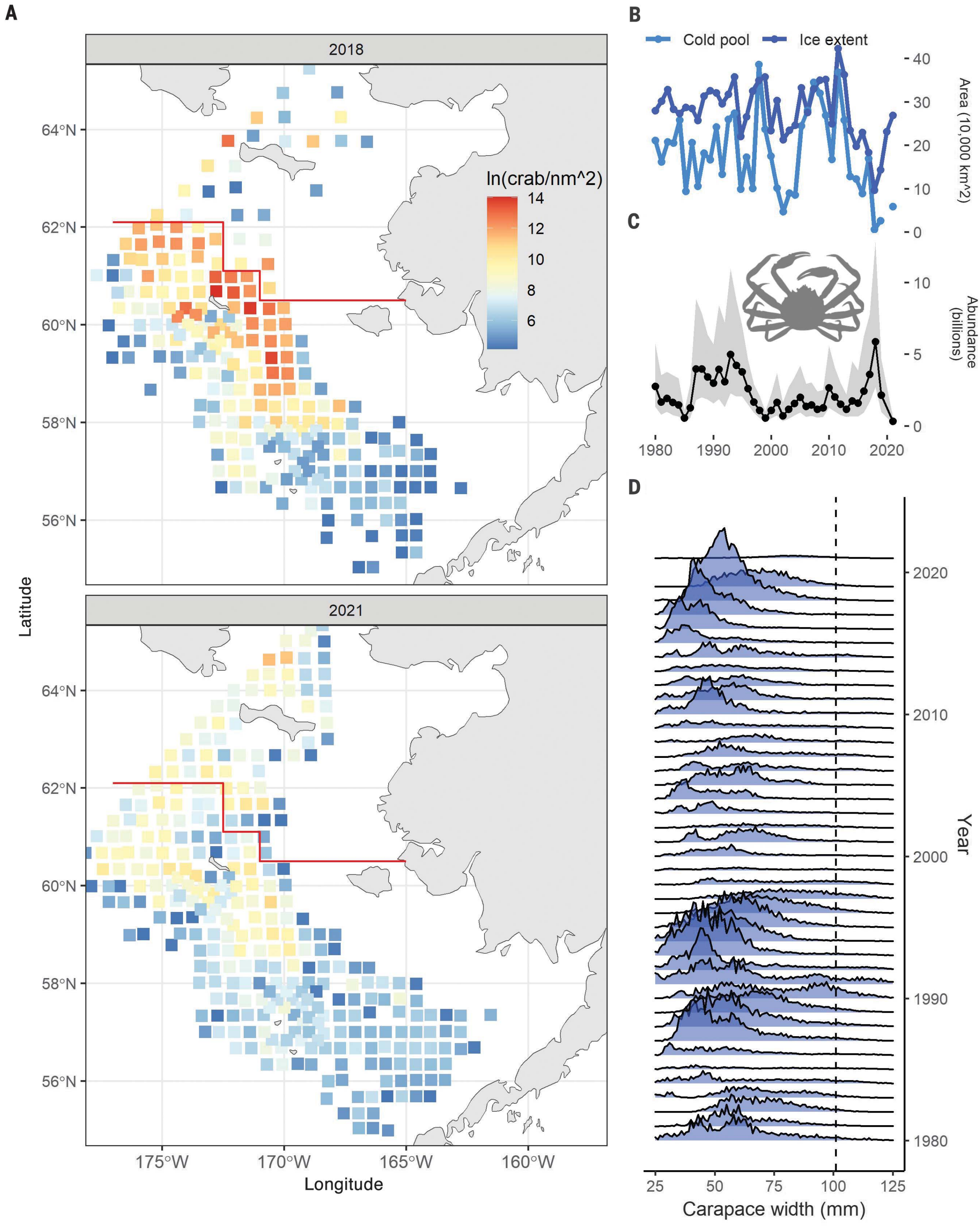

Fig. 1. The collapse of the snow crab population in the eastern Bering Sea. (**A**) Snow crab are widely distributed on the eastern Bering Sea shelf, and densities of crab were an order of magnitude lower in 2021 compared with 2018. Each square indicates a survey tow with snow crab present, and the red line separates the northern Bering Sea survey and eastern Bering Sea survey extent. lat, latitude; lon, longitude. (**B** and **C**) Changes in ice extent and (B) the resulting cold pool area influence (C) the population dynamics of snow crab. Only male abundance is plotted; shading indicates the 95% confidence intervals. (**D**) The relative numbers at size of crab observed in the survey over time. The vertical dashed line indicates the size at which the fishery begins to retain crab. Smaller crab are poorly captured by the survey gear, so the true size of a cohort is not apparent until a few years after it is first observed in the survey—compare 2015 with 2018, for example.

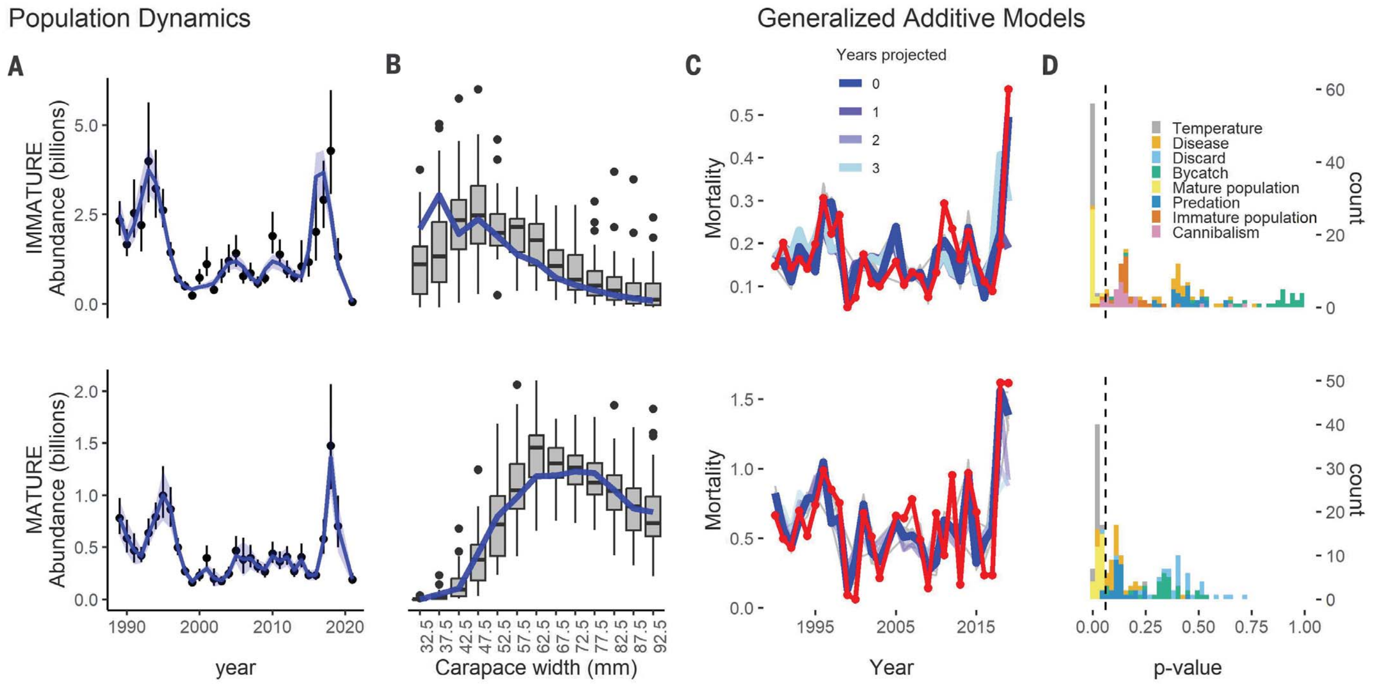

Fig. 2. Population dynamics fits and covariate relationships with mortality. Population dynamics model fits to the survey data. The top row relates to immature crab; the bottom row relates to mature crab. (**A**) Points and vertical lines indicate observed abundances, and estimates are shown in blue, with 95% confidence intervals shaded in light blue. (**B**) Box plots are size composition data aggregated over the study period with average estimated size composition over year by size shown in blue. (**C**) Fits (blue) to estimated mortality (red) from GAMs with (**D**) the significance of covariates resulting from replicates over leave-one-out cross validation. Lighter shades of blue in (C) are fits of the model with a given number of years excluded from the end of the time series and then predicting the held-out data.

but several observations corroborate the idea that temperature and population density were the key variables in the recent collapse. Cod predation was near average levels during the collapse when considering the number of snow crab in the system, and for a portion of the year, a large fraction of the cod population moved out of the eastern Bering Sea into the northern Bering Sea, which rarely occurs. This movement would serve to decrease the already average predation on snow crab in our study area. Furthermore, the missing snow crab were of a size that is larger than cod usually eat in large numbers. Trawling pressure has been another oft-raised potential cause of the collapse, but trawling activity in the Bering Sea has been relatively consistent over the past ~20 years. The observed bycatch of snow crab by trawlers was several times lower during the collapse than historical highs, and estimated mortality was low during the historical periods of high bycatch. This observation, coupled with the largest cohort in history having established and grown on the sea shelf for ~8 years under consistent trawling pressure, are difficult to reconcile with the idea that trawling contributed to the collapse. A more in-depth discussion of these points is available in the supplementary text.

Assessing the predictive skill of a model is an important check on overfitting and is relevant to providing management advice. After an ecologically and economically costly collapse, it is natural to ask whether we could have foreseen the collapse. To explore this question, we excluded 1, 2, and 3 years of data from the end of the time series; refitted the models; then tried to predict the excluded years of mortality with the covariates from those years. The model for immature mortality contained enough information in 2016 to forecast an increase in mortality, but it was not able to reach the magnitude of the estimated mortality in 2019 (Fig. 2C). The model for mature mortality performed similarly, forecasting an increase in mortality over the projection period, but it was not able to reach the estimated mortalities until the most recent data were included in the model. This suggests that the circumstances underpinning the recent collapse were unprecedented in the Bering Sea in recent history.

The collapse of the eastern Bering Sea snow crab population appears to be one of the largest reported losses of motile marine macrofauna to marine heatwaves globally (*11*), exacerbated by the record number of snow crab in the ecosystem. However, the thermal limits of snow crab exceed the observed temperatures (*6*). Temperature-dependent caloric requirements are a potential explanation to relate temperature to mortality. Foyle *et al.* (*6*) showed that caloric requirements for snow crab in the laboratory nearly double from 0°C to 3°C, which is roughly the change experienced by immature crab from 2017 to 2018 (Fig. 3A). Caloric requirements in 2018 (calculated from temperature occupied, abundance of crab at size, and weight at size) quadrupled for the modeled fraction of snow crab in the eastern Bering Sea from 2017 and were double the previous maximum value in 1989 (Fig. 3B). The impact of increased caloric demands appears to be reflected in the observed weight at size. A crab with a 75-mm carapace width in 2018 weighed on average 156 g and was ~25 g lighter (~15% of its body weight) than a crab in 2017 of the same size in the same-temperature waters (Fig. 3C). Furthermore, the spatial footprint of the stock was near the lowest levels historically in 2018 (Fig. 3, D and E). The unprecedented caloric demands, coupled with a small area from which to forage relative to historical grounds, suggest that starvation likely played a role in the disappearance of more than 10 billion snow crab, similar to the marine heatwave–related collapse of Pacific cod in the Gulf of Alaska in 2016 (*12*).

The eastern Bering Sea snow crab population collapsed once before in the late 1990s, but that collapse arose from a lack of recruitment, not a sudden mortality event. The Arctic Oscillation and sea ice have been linked to

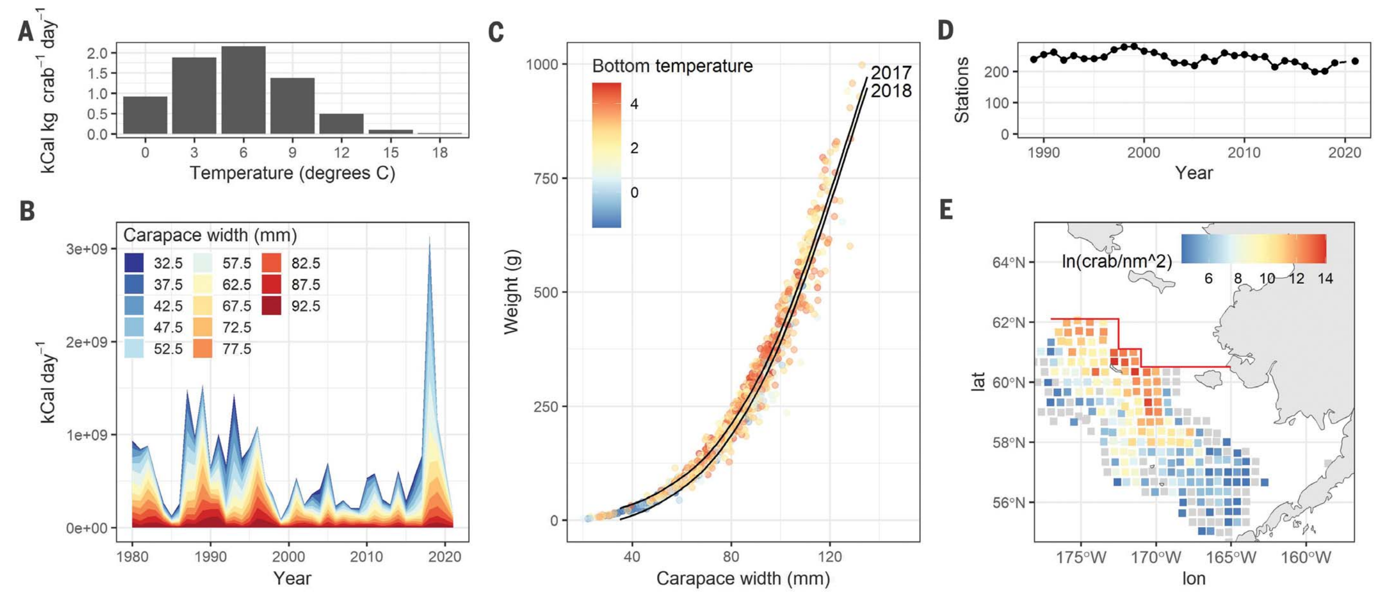

Fig. 3. Influence of temperature on snow crab metabolism, body condition, and distribution. (**A**) Impact of temperature on caloric requirements for snow crab in the laboratory. [Reproduced from Foyle *et al.* (*6*).] (**B**) The extrapolated caloric requirements for crab in the eastern Bering Sea based on temperature, abundance at size, and weight at size. (**C**) The observed weight at size colored by the temperature (°C) at which the crab were collected. The lines indicate the relationship between weight at size in 2017 and 2018 while holding temperature at 1°C. (**D**) The spatial extent of the stock has varied over time, as seen through the number of stations at which crab were observed in the 400-square-nautical-mile grid. (**E**) Distribution in 2018 (colored tiles) was one of the smallest on record (gray tiles indicate maximum historical range).

snow crab recruitment, and projections of recruitment suggest that snow crab abundances will decline in the future as sea ice disappears from the eastern Bering Sea (*13*). However, these declines were projected to occur at least 20 years from now. Given the recent collapse, the short-term future of snow crab in the eastern Bering Sea is precariously uncertain. Over the long term, the northern Bering Sea is a prospective climate refuge for snow crab (and potentially a fishery) (*14*), but the possibility of a fishery rests on the unclear prospect of crab growing to a larger size in the north and the currents retaining pelagic larvae released in the northern Bering Sea.

In 2020 and 2021, 59 boats fished for snow crab, which brought $227 million (ex-vessel) into fishing communities (*15*). The disappearance of snow crab will be a staggering blow to the functioning of some communities in rural Alaska, such as those on Saint Paul Island, which rely strongly on the revenue derived from the capture and processing of snow crab. The Magnuson-Stevens Act includes provisions for fisheries disaster assistance, which were designed to provide economic support for communities who face hardship as a result of collapsed fisheries. The number of applications in the United States has been increasing in recent years (*16*), and an application for snow crab was received in early 2022. These funds are a boon in the medium term, but years can pass between disaster and dispersal of these funds. Consequently, Alaskan crabbers face an uncertain short-term future because the disaster funds may not arrive in time to forestall the bankruptcy of long-standing businesses.

Beyond the fishery for snow crab, Alaskan fisheries are some of the most productive in the world; they produced 5.27 billion pounds of seafood in 2021, valued at US$1.9 billion (*17*). The collapse of the snow crab population was a strong response to a marine heatwave, and other populations in the Bering Sea also suffered large losses. Salmon populations in the north collapsed, and seabird and seal die-offs occurred (*18*). However, other populations are flourishing. Sablefish abundances are at all-time highs in the Bering Sea (*19*), and the assessment for walleye pollock, which supports the largest fishery in the Bering Sea and one of the largest in the world (*20*), reported one of the largest estimated year classes established in 2018 (*21*). Pollock may still decline under continued warming (*22*), but the short-term response to markedly warmer bottom waters was a population boom. The adaptive capacity of species is a key uncertainty in the outcome of warming oceans, but it is very probable that the benthic community in the eastern Bering Sea in the not-too-distant future will look different from today's given the rapid pace of warming (*23*).

Overfishing has historically been the largest threat to global fisheries, but in many parts of the world, this problem has been addressed with careful management (*1*). Climate change is the next existential crisis for fisheries, and snow crab are a prime example for how quickly the outlook can change for a population. In 2018, catches were projected to increase to levels not seen in decades. Three years later, the population had collapsed. Our current management tools base management targets and projected sustainable yields on the historical dynamics of a population. However, projections based on historical dynamics are unreliable when the future environmental conditions of a region will not resemble the past. Incorporating environmental drivers into management targets has been a recent focus of the scientific literature, but this can result in counterintuitive management responses such as increasing exploitation rates on populations undergoing climate-related declines in productivity (*24*). Our experience in the management of a collapsing snow crab population suggests that considering environmental influence in estimates of biomass used to set catch limits can be important, but how to consider environmental change in management targets is an unresolved question.

Beyond reconsidering how sustainable catches and management targets are calculated under widespread changes in productivity, other practical matters need close attention from fisheries managers and stakeholders. These include (i) enacting efficient and timely disaster response with plans for the possibility that a "disaster" is permanent, (ii) implementing management institutions that allow fishers to pursue diverse portfolios of species, and (iii) ensuring consistent and timely biological surveys. Support for the development of alternative marine-based livelihoods (such as mariculture) may also alleviate some of the pressures associated with fishery collapses. The Bering Sea is on the frontlines of climate-driven ecosystem change, and the problems currently faced in the Bering Sea foreshadow the problems that will need to be confronted globally.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adf6035
Materials and Methods
Supplementary Text
Figs. S1 to S51
Tables S1 to S6
References (*26*–*45*)
MDAR Reproducibility Checklist

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