



## MARINE HEATWAVES

## The collapse of eastern Bering Sea snow crab

Cody S. Szuwalski<sup>1\*</sup>, Kerim Aydin<sup>1</sup>, Erin J. Fedewa<sup>2</sup>, Brian Garber-Yonts<sup>1</sup>, Michael A. Litzow<sup>2</sup>

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.

**S**now 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, winter 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).

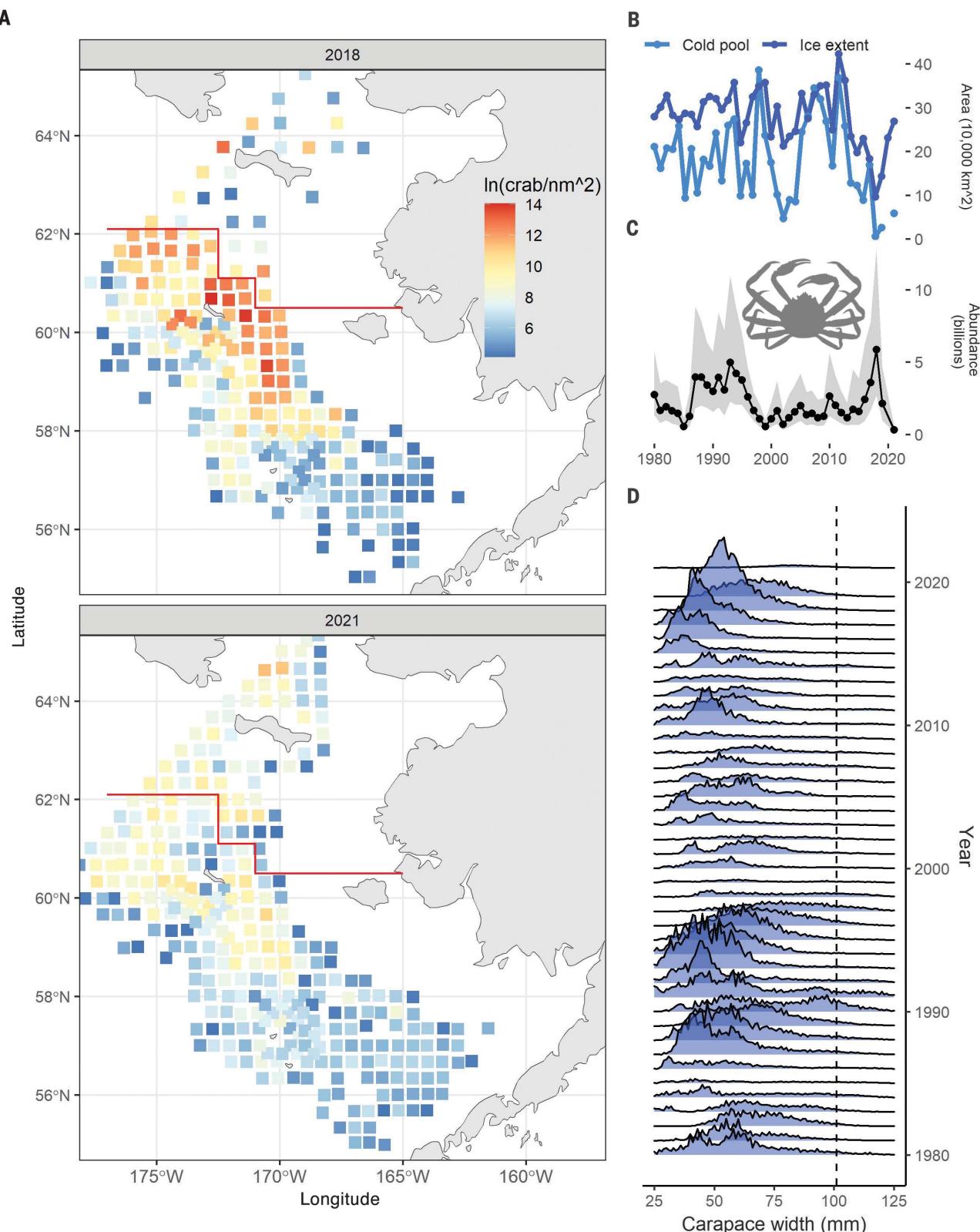
The population dynamics model fitted the indices of abundance and size composition data from the survey well, which is not unexpected, given the flexibility of the model (Fig. 2, A and B). Estimated mortality was higher and more varied for mature crab than for immature crab, and estimated mortalities 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,

<sup>1</sup>Alaska Fishery Science Center, National Oceanic and Atmospheric Administration, Seattle, WA, USA. <sup>2</sup>Alaska Fishery Science Center, National Oceanic and Atmospheric Administration, Kodiak, AK, USA.

\*Corresponding author. Email: cody.szuwalski@noaa.gov

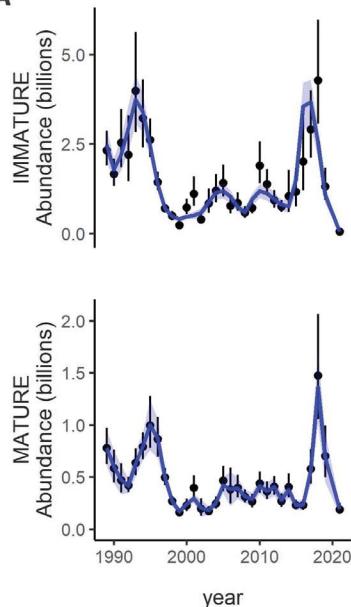
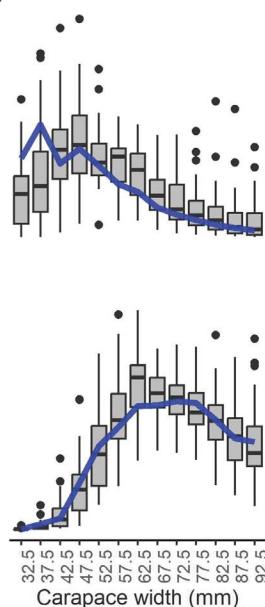


**Fig. 1. The collapse of the snow crab population in the eastern Bering Sea.**

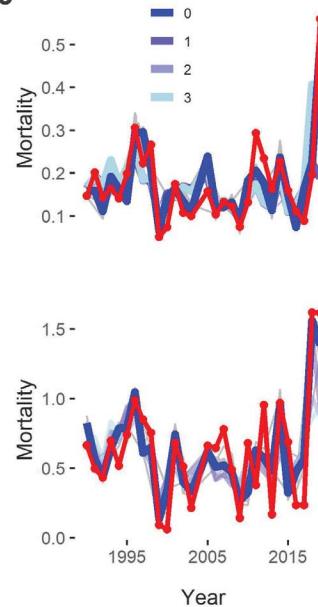
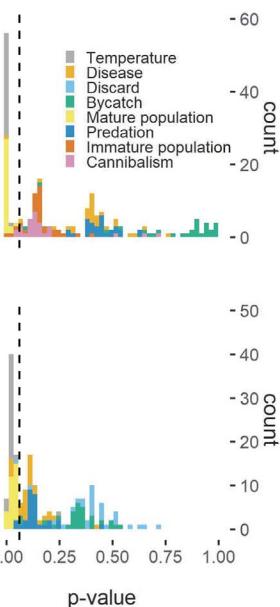
(A) Snow crab are widely distributed on the eastern Bering Sea shelf, and densities of crab were an order of magnitude lower in 2021 compared with 2018. Each square indicates a survey tow with snow crab present, and the red line separates the northern Bering Sea survey and eastern Bering Sea survey extent. 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.

## Population Dynamics

**A****B**

## Generalized Additive Models

**C****D****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

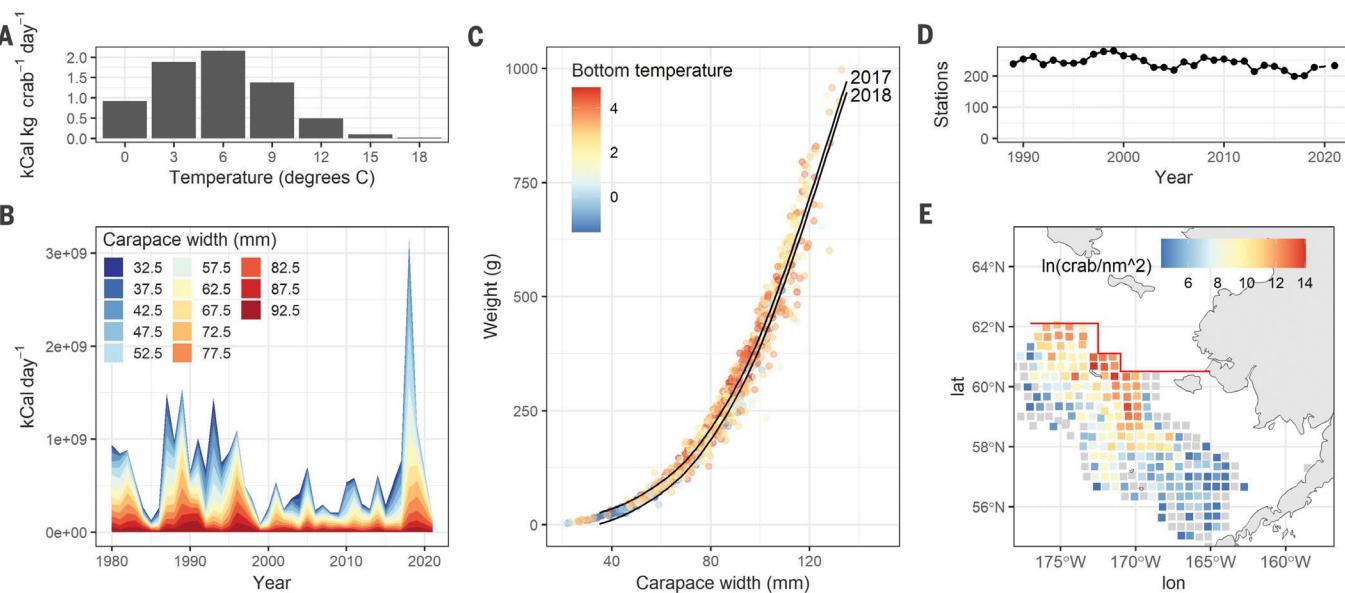
over the study period with average estimated size composition over year by size shown in blue. (C) Fits (blue) to estimated mortality (red) from GAMs with (D) the significance of covariates resulting from replicates over leave-one-out cross validation. Lighter shades of blue in (C) are fits of the model 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.

## REFERENCES AND NOTES

1. R. Hilborn *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **117**, 2218–2224 (2020).
2. L. A. Copeman *et al.*, *Polar Biol.* **44**, 1883–1901 (2021).
3. C. S. Szuwalski, "Stock assessment of Eastern Bering Sea snow crab. Stock assessment and fishery evaluation report for the king and tanner crab fisheries of the Bering Sea and Aleutian Islands regions" (North Pacific Fishery Management Council, 2021).
4. I. S. Chernienko, *Izvestiya TINRO* **210**, 359–370 (2021).
5. G. R. Hoff, "Results of the 2016 eastern Bering Sea upper continental slope survey of groundfish and invertebrate resources," NOAA technical memorandum NMFS-AFSC-339 (2016).
6. T. P. Foyle, R. K. O'Dor, R. W. Elner, *J. Exp. Biol.* **145**, 371–393 (1989).
7. G. M. Lang, P. A. Livingston, "Food habits of key groundfish species in the eastern Bering Sea slope regions," NOAA technical memorandum NMFS-AFSC-67 (1996).
8. G. A. Lovrich, B. Sainte-Marie, *J. Exp. Mar. Biol. Ecol.* **211**, 225–245 (1997).
9. T. R. Meyers *et al.*, *Dis. Aquat. Organ.* **26**, 221–227 (1996).
10. S. N. Wood, *J. R. Stat. Soc. Series B Stat. Methodol.* **73**, 3–36 (2011).
11. K. E. Smith *et al.*, *Ann. Rev. Mar. Sci.* **15**, 119–145 (2023).
12. S. J. Barbeaux, K. Holsman, S. Zador, *Front. Mar. Sci.* **7**, 703 (2020).
13. C. S. Szuwalski *et al.*, *ICES J. Mar. Sci.* **78**, 502–515 (2020).
14. E. J. Fedewa, T. M. Jackson, J. Richar, J. L. Gardner, M. A. Litzow, *Deep Sea Res. Part II Top. Stud. Oceanogr.* **181–182**, 104878 (2020).
15. B. Garber-Yonts, J. Lee, "SAFE report for the king and tanner crab fisheries of the Gulf of Alaska and Bering Sea/Aleutian Islands Area: Economic status of the BSAI king and tanner crab fisheries off Alaska, 2021" (North Pacific Fishery Management Council, 2021).
16. L. Bellquist, V. Saccomanno, B. X. Semmens, M. Gleason, J. Wilson, *PeerJ* **9**, e11186 (2021).
17. NOAA Fisheries, *Fisheries of the United States Report* (NOAA, 2022); <https://www.fisheries.noaa.gov/foss>.
18. E. C. Siddon, S. G. Zador, G. L. Hunt Jr., *Deep Sea Res. Part II Top. Stud. Oceanogr.* **181–182**, 104914 (2020).
19. D. Goethel *et al.*, "Assessment of the sablefish stock in Alaska. NPFMC Bering Sea, Aleutian Islands and Gulf of Alaska Stock Assessment and Fishery Evaluation report" (North Pacific Fishery Management Council, 2022).
20. Food and Agriculture Organization, *The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation* (Food and Agriculture Organization, 2022).
21. J. Ianelli *et al.*, "Assessment of the walleye pollock stock in the eastern Bering Sea. NPFMC Bering Sea, Aleutian Islands and Gulf of Alaska Stock Assessment and Fishery Evaluation report" (North Pacific Fishery Management Council, 2022).
22. F. Mueter, N. Bond, J. Ianelli, A. Hollowed, *ICES J. Mar. Sci.* **68**, 1284–1296 (2011).
23. M. Rantanen *et al.*, *Commun. Earth Environ.* **3**, 168 (2022).
24. C. S. Szuwalski *et al.*, *Fish Fish.* **24**, 439–453 (2023).
25. C. S. Szuwalski, K. Aydin, E. J. Fedewa, B. Garber-Yonts, M. A. Litzow, The collapse of eastern Bering Sea snow crab Zenodo (2023); <https://zenodo.org/record/8184862>.

## ACKNOWLEDGMENTS

We thank the Resource Assessment and Conservation Engineering Division and the Kodiak Shellfish Assessment Program, at the Alaska Fisheries Science Center, and the Alaska Department of Fish and Game for long-term data collection efforts, without which analyses such as this would be impossible. We also thank the Bering Sea Fisheries Research Foundation for selectivity data from their trawl experiments. A. Hollowed, S. Zador, L. Barnett, S. Barbeaux, the members of the North Pacific Fishery Management Council's Crab Plan Team, the Science and Statistical Committee, and three anonymous reviewers provided comments that improved this manuscript. **Author contributions:** Conceptualization: C.S.S., K.A., E.J.F., B.G.-Y., and M.A.L. Methodology: C.S.S. and K.A. Formal analysis: C.S.S. Investigation: C.S.S., K.A., E.J.F., B.G.-Y., and M.A.L. Visualization: C.S.S. Writing – original draft: C.S.S. Writing – review and editing: C.S.S., K.A., E.J.F., B.G.-Y., and M.A.L. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** A repository including the data and code used to perform the analysis can be found at (25). **License information:** Copyright © 2023 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

## SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.adf6035](https://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

Submitted 4 November 2022; accepted 31 August 2023  
10.1126/science.adf6035

## The collapse of eastern Bering Sea snow crab

Cody S. Szuwalski, Kerim Aydin, Erin J. Fedewa, Brian Garber-Yonts, and Michael A. Litzow

Science 382 (6668), . DOI: 10.1126/science.adf6035

### Editor's summary

Marine heatwaves, a component of our impact on the Earth's climate, can bring both expected and unexpected environmental change. Between 2018 and 2021, after a period of historically high crab abundance and a series of marine heatwaves, the population of snow crab in the Bering Sea declined by 10 billion. Szuwalski *et al.* used survey data to model the potential drivers of the decline in this ecologically and commercially important species. They found that the temperature of the water was not above the species' thermal limits, but it did increase their caloric needs considerably (see the Perspective by Kruse). This increase, in conjunction with a restriction in range, led to an unexpected mass starvation event. —SNV

### View the article online

<https://www.science.org/doi/10.1126/science.adf6035>

### Permissions

<https://www.science.org/help/reprints-and-permissions>



## Supplementary Materials for The collapse of eastern Bering Sea snow crab

Cody S. Szuwalski *et al.*

Corresponding author: Cody S. Szuwalski, cody.szuwalski@noaa.gov

*Science* **382**, 306 (2023)  
DOI: 10.1126/science.adf6035

### The PDF file includes:

Materials and Methods  
Supplementary Text  
Figs. S1 to S51  
Tables S1 to S6  
References

### Other Supplementary Material for this manuscript includes the following:

MDAR Reproducibility Checklist

## Supplementary materials for ‘The collapse of eastern Bering Sea snow crab’

4 **Contents**

5	<b>Supplementary materials</b>	1
6	Methods overview . . . . .	1
7	Population dynamics model . . . . .	1
8	Survey selectivity . . . . .	3
9	Objective function . . . . .	3
10	Penalties and priors . . . . .	4
11	Population dynamics model sensitivities . . . . .	4
12	Does allowing mortality or catchability to vary over time improve model fits? . . . . .	4
13	How well can the model estimate mortality and selectivity with simulated data? . . . . .	5
14	How do the assumptions about weighting and priors influence the estimated quantities? . . . . .	6
15	Covariate construction . . . . .	6
16	Temperature . . . . .	7
17	Predation . . . . .	7
18	Disease . . . . .	8
19	Cannibalism . . . . .	8
20	Fisheries data . . . . .	9
21	Crab density . . . . .	9
22	Generalized additive models . . . . .	9
23	Sensitivities to model assumptions in GAMs . . . . .	11
24	Error structure . . . . .	11
25	Does incorporating the uncertainty in the estimates of mortality change analysis outcomes? . . . . .	11
26	Shape of estimated relationships . . . . .	12
27	How could temperature relate to mortality mechanistically? . . . . .	12
28	A word on methods . . . . .	14
29	Frequently asked questions . . . . .	14
30	Are you sure the collapse wasn't a result of cod predation? . . . . .	14
31	Are you sure the collapse wasn't a result of trawling? . . . . .	15
32	What do crab eat? If they starved, did there appear to be large declines in their prey base? . . . . .	15

33	If it was a large mortality event, did you see large numbers of empty carapaces in the survey?	15
34	Were that many crab really in the eastern Bering Sea to begin with? Was the ‘collapse’ an	
35	artifact of some survey error? . . . . .	16

## 36 Supplementary materials

### 37 Methods overview

38 We used an integrated population model to estimate variation in mortality over time for snow crab in the  
 39 eastern Bering Sea and generalized additive models (GAMs) to relate the estimated variation in mortality  
 40 to potential stressors in the environment. The population dynamics model was fit to abundance and size  
 41 composition data from the National Marine Fisheries Service (NMFS) summer bottom trawl survey on the  
 42 eastern Bering Sea shelf to estimate total mortality by maturity state and year for male snow crab. We  
 43 then developed indices for temperature occupied, disease prevalence, cannibalism, and crab density from the  
 44 NMFS survey to test as covariates in GAMs. Cod predation indices were developed using stomach content  
 45 data collected on NMFS surveys in addition to cod size composition and abundances. Indices for fishery  
 46 related effects were collated from fisheries statistics from the Alaska Department of Fish and Game and also  
 47 included in the GAMs.

48 Ecological detective work in the marine environment is hampered by the difficulty of observation and this is  
 49 particularly so on the eastern Bering Sea shelf. The waters in which snow crab reside range from 50-200 meters  
 50 deep and are seasonally covered by ice, making data collection only feasible in the summer. Consequently,  
 51 the survey based portions of our analyses are derived from a yearly snapshot of the population over an  
 52 approximately 30 year period. Each of the hypotheses explored here clearly result in some mortality. We  
 53 know that millions of crab are eaten by cod every year, the directed and bycatch fisheries kill crab, larger  
 54 crab eat smaller crab, and crab die from bitter crab disease each year. The goal of our analysis is to place  
 55 each of these processes in a historical context to try to understand the relative impact of each and what  
 56 was different about the recent collapse. More than one way exists to analyse the available data on this  
 57 issue. Below we describe our approach, including a description of each of the components of our analysis,  
 58 a discussion of the rationale behind our modeling decisions, and sensitivities and simulation tests of our  
 59 models, all of which provide what we think is sound reasoning for our analysis.

### 60 Population dynamics model

61 The population dynamics model presented here incorporated the best available information on relevant  
 62 population processes to estimate total mortality for male snow crab on the eastern Bering Sea shelf and is  
 63 similar in structure to the model used to assess eastern Bering Sea snow crab for management (Szuwalski,  
 64 2021). The model tracked numbers of male crab at size at maturity state over time with size bins ranging  
 65 from 30-95 mm carapace width with 5 mm bin widths. Only male crab were modeled because male and  
 66 female crab appear to have somewhat different dynamics and the male crab in the modeled size range are  
 67 better selected by the survey gear (Szuwalski, 2021). Snow crab are sexually dimorphic, with male snow crab  
 68 growing to nearly twice the size of females, which accounts for the better selection in the survey. Only crab  
 69 smaller than 95 mm were modeled for two reasons: 1) to attempt to isolate the effect of the directed fishery  
 70 (crab of >101 mm carapace width are targeted in the fishery; discussed further below) and 2) almost all of  
 71 the crab that disappeared since 2018 are in this size range. The population dynamics model operates on a  
 72 half year time step, starting in July at the time of the NMFS survey. Total mortality ( $Z$ ) is estimated by  
 73 year ( $y$ ) and maturity state ( $m$ ). Other estimated parameters include the initial numbers at size by maturity  
 74 state, yearly log recruitments, a vector of scalars that determine the proportions of estimated recruitment  
 75 split into the first two size bins, and a variance component for the penalty on total mortality. Parameters  
 76 determining growth, maturity, and survey selectivity were estimated outside of the model and specified when  
 77 estimating mortality and catchability. Mortality is the only population process that occurs in the first half  
 78 of a given year:

$$N_{t=y+0.5,s,m} = N_{t=y,s,m} e^{-Z_{t,s,m}/2} \quad (1)$$

79 Growth occurs at the beginning of the second half of the year for immature crab and is represented in the  
 80 model by multiplying the vector of immature crab at size by a size-transition matrix  $X_{s,s'}$  that defines the  
 81 size to which crab grow given an initial size. Snow crab are observed to undergo a ‘terminal molt’ to maturity  
 82 after which growth ceases (Tamone et al., 2005). Accordingly, all immature crab are assumed to molt and no  
 83 mature crab molt in our model. The newly molted crab are assigned to a maturity state based on observed  
 84 ogives of the proportion of mature new shell males by size calculated from chelae height measured in the  
 85 NMFS survey data (Otto, 1998), which varies over time ( $\rho_{y,s}$ ; Figure S4). The average probability of having  
 86 undergone terminal molt is used in years during which data were not collected. This process results in two  
 87 temporary vectors of numbers at size:

$$n_{t=y+0.5,s,m=1} = \rho_{y,s} X_{s,s'} N_{t=y+0.5,s,m=1} \quad (2)$$

$$n_{t=y+0.5,s,m=2} = (1 - \rho_{y,s}) X_{s,s'} N_{t=y+0.5,s,m=2} \quad (3)$$

88 The size transition matrix  $X_{s,s'}$  was constructed using growth increment data collected over several years  
 89 (see Szuwalski [2021] for a summary) to estimate a linear relationship between pre- and post-molt carapace  
 90 width (Figure S5), ( $\hat{W}_{s,w}^{pre}$  and  $\hat{W}_{s,w}^{post}$ , respectively) and the variability around that relationship was charac-  
 91 terized by a discretized and renormalized normal distribution with a size-varying standard deviation,  $Y_{s,w,w'}$ ,  
 92 (Figure S5).

$$X_{s,w,w'} = \frac{Y_{s,w,w'}}{\sum_{w'} Y_{s,w,w'}} \quad (4)$$

$$Y_{s,w,w'} = (\Delta_{w,w'})^{\frac{L_{s,w} - (\bar{W}_w - 2.5)}{\beta_s}} \quad (5)$$

$$\hat{L}_{s,w}^{post} = \alpha_s + \beta_{s,1} \text{hat} W_{s,w}^{pre} \quad (6)$$

$$\Delta_{w,w'} = \bar{L}_{w'} + 2.5 - W_w \quad (7)$$

94 It is important to note that crab can ‘outgrow’ this model, which is represented by the pre-molt-carapace  
 95 widths (e.g. 87.5 and 92.5 mm carapace width in Figure S5) that have low probability of molting to any of  
 96 the sizes that are included in the population dynamics model.

97 Recruitment by year,  $\tau_y$ , was estimated as a vector in log space and added to the first two size of classes of  
 98 immature crab based on another estimated vector  $\delta_y$  that determines the proportion allocated to each size  
 99 bin.

$$n_{t=y+0.5,s=1,m=1} = n_{t=y+0.5,s,m=1} + \delta_y e_y^\tau \quad (8)$$

$$n_{t=y+0.5,s=2,m=1} = n_{t=y+0.5,s,m=1} + (1 - \delta_y) e_y^\tau \quad (9)$$

100 Finally, the last half of the year of mortality is applied to the population after growth, molting, and recruit-  
 101 ment occurs. Note that this allows a crab to experience two different mortalities within a given year as it  
 102 undergoes terminal molt.

$$N_{t=y+1,s,m=1} = n_{t=y+0.5,s,m=1} e^{-Z_{t,s,m}/2} \quad (10)$$

$$N_{t=y+1,s,m=2} = (N_{t=y+0.5,s,m=2} + n_{t=y+0.5,s,m=2}) e^{-Z_{t,s,m}/2} \quad (11)$$

105 **Survey selectivity**

106 The observed numbers of crab at size by year in the NMFS survey reflect the ability of the trawl gear to  
107 capture the crab, also known as ‘selectivity’. The selectivity of trawl gear can change according to size, and  
108 consequently needs to be accounted for in the population dynamics model when fitting to the survey data.  
109 Values for survey selectivity at size were specified using data from experimental *Nephrops* trawls (a small  
110 trawl net designed to maintain bottom contact), operated by the Bering Sea Fisheries Research Foundation  
111 in collaboration with the NMFS summer survey. The experimental trawls were performed at the same time  
112 and location as the NMFS summer survey tows to evaluate the efficiency of the NMFS survey trawl gear  
113 at capturing snow crab (Somerton et al., 2013). The *Nephrops* gear used by the BSFRF was assumed to  
114 capture all crab in its path given strong bottom contact. The resulting area-swept estimates of numbers of  
115 crab at size from the BSFRF and NMFS surveys ( $\hat{N}_{y,s,NMFS}$  and  $\hat{N}_{y,s,BSFRF}$ , respectively) can be used to  
116 infer the selectivity of the NMFS gear in year  $y$  as:

$$S_{y,NMFS} = \frac{\hat{N}_{y,s,NMFS}}{\hat{N}_{y,s,BSFRF}} \quad (12)$$

117 The experimental trawls captured snow crab in the years 2010, 2011, 2016, 2017, and 2018, but the spatial  
118 foot print and sample sizes varied by year (Figure S6). The calculated selectivities by size and by year were  
119 fairly consistent for snow crab of carapace widths 40 - 95 mm, but the signal was less consistent for crab  
120 larger than ~100 mm carapace width (Figure S7). The selectivity of large crab determines the estimated  
121 scale of the population in a population dynamics model, but the information we have on selectivity of large  
122 crab is poor and different assumptions about selectivity lead to very different inference about the stock  
123 (Szuwalski, 2021b). The lack of clear information on the scale of the population exploited by the fishery is  
124 one of the key reasons we used the range of sizes included in this model and excluded the directed fishery  
125 data from the analysis. A GAM was fit through the estimates of selectivity and the resulting estimates by  
126 size were directly specified in the population dynamics model.

127 ‘Catchability’ represents the fraction of the population available to the survey gear (either as a result of  
128 spatial mis-match or the inability of the gear to come in contact with the animals as a result of burrowing  
129 or hiding in untrawlable habitat). The capability for modeling time-varying catchability was built into the  
130 model in the form of a vector of parameters equal to the length of the time series of data. When time-  
131 varying catchability was estimated, the yearly catchability parameters were used to scale the selectivity  
132 curve described above up or down.

133 **Objective function**

134 The objective function for the population dynamics model consists of likelihood components (representing  
135 the fit of the model to the data) and penalty components (which incorporate constraints in the fitting based  
136 on prior information) that are summed and minimized in log space to estimate parameters within the model.  
137 Several data sources were fit to using the following likelihoods. Observed size composition data for immature  
138 and mature males were fit using multinomial likelihoods and were implemented in the form:

$$L_x = \lambda_x \sum_y N_{x,y} \sum_l p_{x,y,l}^{obs} \ln(\hat{p}_{x,y,l} / p_{x,y,l}^{obs}) \quad (13)$$

139  $L_x$  was the likelihood associated with data component  $x$ , where  $\lambda_x$  represented an optional additional weight-  
140 ing factor for the likelihood,  $N_{x,y}$  was the sample sizes for the likelihood,  $p_{x,y,l}^{obs}$  was the observed proportion  
141 in size bin  $l$  during year  $y$  for data component  $x$ , and  $\hat{p}_{x,y,l}$  was the predicted proportion in size bin  $l$  during  
142 year  $y$  for data component  $x$ . Sample sizes were input as 50.

143 Observed indices of abundance for immature and mature males were fit with log normal likelihoods imple-  
144 mented in the form:

$$L_x = \lambda_x \sum_y \frac{(\ln(\hat{I}_{x,y}) - \ln(I_{x,y}))^2}{2(\ln(CV_{x,y}^2 + 1))} \quad (14)$$

<sup>145</sup>  $L_x$  was the contribution to the objective function of data component  $x$ ,  $\lambda_x$  was any additional weighting  
<sup>146</sup> applied to the component,  $\hat{I}_{x,y}$  was the predicted value of quantity  $I$  from data component  $x$  during year  $y$ ,  
<sup>147</sup>  $I_{x,y}$  was the observed value of quantity  $I$  from data component  $x$  during year  $y$  and  $CV_{x,y}$  was the coefficient  
<sup>148</sup> of variation for data component  $x$  during year  $y$ .

#### <sup>149</sup> Penalties and priors

<sup>150</sup> Smoothing penalties were placed on estimated vectors of deviations for immature and mature natural mor-  
<sup>151</sup> tality (and immature and mature catchability in the simulation analyses aimed at understanding the es-  
<sup>152</sup> timability of mortality and catchability) using normal likelihoods on the second differences of the vectors.  
<sup>153</sup> Normal priors were also placed on the mean value of natural mortality and catchability and the deviation  
<sup>154</sup> of the estimated mortality from that mean. A prior value of 0.27 is used for the average natural mortality  
<sup>155</sup> based on assumed maximum age of 20 and Hamel's (2015) empirical analysis of life history correlates with  
<sup>156</sup> natural mortality. The priors used for catchability were derived from the selectivity experiments described  
<sup>157</sup> above. The normal priors were of the form:

$$P_x = \lambda_x \sum_y \frac{((\hat{I}_{x,y}) - (I_{x,y}))^2}{CV_{x,y}^2} \quad (15)$$

<sup>158</sup>  $P_x$  was the contribution to the objective function of the penalty associated with model estimate  $x$ ,  $\lambda_x$  was  
<sup>159</sup> any additional weighting applied to the component,  $\hat{I}_{x,y}$  was the predicted value of population process  $I$   
<sup>160</sup> relevant to penalty  $x$  during year  $y$ ,  $I_{x,y}$  was the prior value of process  $I$  relevant to penalty  $x$  during year  $y$   
<sup>161</sup> and  $CV_{x,y}$  was the input coefficient of variation for penalty  $x$  during year  $y$ .

<sup>162</sup> An example of the way in which these equations were implemented can be seen in lines 132-218 of  
<sup>163</sup> 'snow\_down.TPL' in our github repo 'snow\_down/models/model\_vary\_m'.

#### <sup>164</sup> Population dynamics model sensitivities

<sup>165</sup> Modeling decisions are necessarily made in the process of writing population dynamics models and it is  
<sup>166</sup> possible for these decisions to influence the outcome of an analysis. Within the context of our model, these  
<sup>167</sup> decisions include what processes to allow to vary over time, the weights assigned to different data sources  
<sup>168</sup> and penalties in the objective function, which parameters to place priors or penalties on, and what those  
<sup>169</sup> priors or penalties should be. We ran several sensitivity analyses to understand the implications of these  
<sup>170</sup> modeling decisions on the outcome of our analysis.

#### <sup>171</sup> Does allowing mortality or catchability to vary over time improve model fits?

<sup>172</sup> Catchability and mortality are somewhat confounded within population dynamics models (Thompson, 1994).  
<sup>173</sup> Fewer crab observed in a given year can be attributed to either crab dying or by crab moving out of the  
<sup>174</sup> surveyed area either by walking out of the boundaries or burying themselves into the substrate. At the same  
<sup>175</sup> time, it is also clear that catchability and mortality likely vary over time in reality in spite of the fact that  
<sup>176</sup> they are often assumed to be time-invariant in population dynamics models (Johnson et al., 2014). Somerton  
<sup>177</sup> et al. (2013) showed that catchability varied somewhat by substrate and depth for snow crab in the EBS.  
<sup>178</sup> The spatial distribution of snow crab varies over time and substrate and depth vary over space, so it follows  
<sup>179</sup> that catchability should also vary over time.

180 We started exploring the impacts on model output of including time-variation in mortality and catchability by fitting a model with no time-variation in mortality or catchability. Then we compared the output  
181 of this model to models that allow time-variation in mortality, catchability, and both processes simultaneously (Figure S8 & Figure S9). The model with no time-variation in mortality or catchability was able to  
182 capture the general trend in immature and mature survey abundance solely through estimating variability  
183 in recruitment. Allowing time-variation in catchability improved the fits to immature survey abundances  
184 more than time-varying mortality, but time-variation in either process improved fits in a similar manner for  
185 mature survey abundances. Mature size composition data were fit similarly for all models, but immature  
186 size composition data were better fit by the models that allowed time-varying catchability (Figure S8). Part  
187 of the reason this difference in fits to immature size composition data occurs is the variability in the first  
188 several size bins resulting from the poor selectivity of the survey for small animals. Sometimes the peaks  
189 seen in larger size classes are reflected in the preceding years' data for the smallest size classes, sometimes  
190 those peaks are not reflected (compare Figure S10 to Figure S11). As a consequence, positive residuals occur  
191 in the smallest size classes when a pseudocohort is consistently seen in large size classes, but not observed  
192 in the smallest size bins (e.g. 1991 vs. 1992; 1997 vs 1998).

193

194 The model without time-variation in mortality or catchability explained 67% of the deviation in the abundance indices, time-varying mortality explained 77%, time-varying catchability explained 94%, and both processes varying explained 99% of the historical deviance. Model selection based on information criteria (e.g. AIC; Akaike, 1974) are often used to identify a model within a suite of models that most parsimoniously fits the data. Adding time-variation in natural mortality or catchability alone improved model fits parsimoniously (AIC of 3434.15 for base model vs. 1593.836 and 1321.486 for time-varying mortality and catchability, respectively). However, adding time-variation in both processes resulted in a higher AIC (1449.275) than implementing time-variation in catchability, owing to the large number of parameters estimated. While catchability and mortality are somewhat confounded, catchability is also confounded with other sorts of error (e.g. observation) and allowing a relatively unconstrained estimation of catchability over time resulted in over-fitting the data, the consequences of which will be seen in simulations below. Even with this paring of potential models, there are several assumptions that could influence the output of our models. The following sensitivities are aimed at exploring the impacts of those assumptions on model output.

## 208 **How well can the model estimate mortality and selectivity with simulated data?**

209 One of the most essential exercises to perform with a population dynamics model before using its output is  
210 to perform a 'self-test' in which data are simulated from the population dynamics model with appropriate  
211 error and then fit to by the model. The goal of this test is to determine whether or not a model can return  
212 the parameter values underlying the simulated data with the available quantity and quality of data. For our  
213 analysis, the ability of the model to estimate mortality and catchability are of particular interest because  
214 they are candidates for use as input into GAMs to attempt to link the estimates to environmental stressors.  
215 Recruitment is also of interest because of its confounding with the other processes.

216 Log-normal error was added to the true underlying abundance from the simulation model with three different  
217 coefficients of variation: 0.01, 0.10, and 0.30. Simulated data sets were generated 100 times under each  
218 observation error scenario and the population dynamics models were fit to them. Two population dynamics  
219 models were fit: one in which time-varying natural mortality was estimated and one in which time-varying  
220 natural mortality and time-varying catchability were estimated. Estimates of mortality were closer to the true  
221 underlying values than estimates of catchability (compare Figure S12 to Figure S13). Mature mortality was  
222 better estimated than immature mortality regardless of data quality or model configuration. The correlation  
223 between estimated and simulated mortality was 0.65 and 0.96 for immature and mature mortality for the  
224 0.01 observation error scenarios, respectively. The ability of the models to estimate mortality became more  
225 similar as data quality decreased. Overall, the model was best able to estimate mature mortality and this is  
226 likely a consequence of its separation from estimated recruitment in time. In general, estimates of catchability  
227 for both maturity states were unreliable.

228 As a result of these simulation analyses, two modeling decisions arose. First, we used estimated variation in  
229 mortality from models that only estimate time-variation in mortality because the estimates of mortality from

models that estimated time-variation in both mortality and catchability were less reliable. This precludes attempts to identify relationships between estimated catchability and environmental variables. Second, the inability of the model to capture the scale of the population (Figure S14) underscores the need to relate mortality to the environmental covariates outside of the model, rather than attempting to build them into the model (similar to Dorn and Barnes, 2022). The covariates described below are indices of a particular environmental stressor, not absolute quantities that could provide scale to the model.

## How do the assumptions about weighting and priors influence the estimated quantities?

Some aspects of the model that may influence the outcome of the fitting are specified by the user with no clear ‘correct’ value. These include the weights assigned to the size composition data, some priors placed on population processes, and the weights assigned to the smoothness penalties. We performed sensitivity analyses for these parameters to check how different specifications changed the fits to the data and the estimates of mortality and catchability. We input a range of values for the size composition weights (25, 50, 100), the prior on the mean natural mortality in log space (-1.6, -1.2, -0.8), the input standard deviation for the penalties on natural mortality (0.01, 0.1, 0.2) and the smoothness penalty on the estimated time series’ of mortalities and catchabilities (0.001, 0.1, 0.5, 0.1).

Differences among sensitivity scenarios resulted in very small changes in the fits to the data (Figure S15), but larger changes in estimated mortalities and catchabilities (Figure S16). The smoothness penalty placed on mortality over time appeared to be the largest driver of changes in estimates of M and q, so we looked at a wider range of smoothness penalties (i.e. 0.001, 0.1, 0.25, 0.5, 1, 5, 10, 1000). Trajectories of mortalities were roughly preserved across this range. The prior on mean natural mortality predictably scaled the estimated time series up or down. The best available information suggests natural mortality should be approximately 0.27 given an assumed (but based on a range of studies; see Szewalski, 2021 for a summary) maximum age of 20 years for wild snow crab. Based on these analyses, we elected to use small smoothing penalties because there is no evidence to suggest that mortality should be particularly smooth from year to year and relatively tight priors on the mean mortality given outside information to support an average mortality value based on longevity. These analyses also underscore the fact that the scale of the population is difficult to estimate with the data available and the need to relate mortality to the environmental covariates outside of the population dynamics model. This likely comes from the fact that recruitment and immature mortality are confounded (i.e. fewer immature crab in a given year can be because of increased immature mortality or because of lower recruitment).

## Covariate construction

A wide range of factors could potentially influence mortality of snow crab on the eastern Bering Sea shelf, including temperature, predation, disease, cannibalism, and fisheries effects. The NMFS summer trawl survey provides a rich spatio-temporal data set to develop time series of temperature occupied, predation, disease, and cannibalism (Zacher et al., 2022). The fisheries-dependent observer data provide spatio-temporal information on bycatch (AKFIN, 2022). The main text notes that more than 10 billion crab have gone missing since 2018. This number is derived from the input total numbers observed in the survey to the assessment, which decreased from 11.7 billion animals in 2018 to 940 million animals in 2021. However, this figure does not account for the selectivity of the survey gear and includes both sexes. If survey selectivity is accounted for, the number of missing crab increases dramatically, with the most recent assessment estimating a decline from ~47 billion in 2017 to 2.58 billion in 2022. Regardless of the metric used, the number of crab missing from the Bering Sea survey was exceptionally large.

Currently, estimating spatially-explicit, time-varying mortality is not computationally feasible, nor are data on movement available to inform such a model. Consequently, our analysis aggregates the spatial data for snow crab into time-series. The end goal is to use these time-series in predictive models to identify relationships between estimated mortality and stressors, so attention has to be paid to creating appropriate comparisons. For example, a predation index needs to consider not only the total consumption of crab by

277 cod, but also the total number of crab in the ocean of the size that can be consumed by cod to be comparable  
278 to changes in estimated mortality rates (discussed more below).

279 Another important point for consideration in covariate construction is the estimation of mortality by maturity  
280 state. Snow crab in the EBS undergo an ontogenetic migration in which juvenile crab settle on the northeast  
281 portion of the shelf after their pelagic phase, then migrate southwest into deeper and (usually) warmer  
282 waters (Ernst et al., 2005; Parada et al., 2010). This means that the conditions and stressors experienced  
283 by immature crab can be different than those by mature crab. To address this issue, the spatial data sets  
284 for temperature, disease, and cannibalism were split based on the size above which half of the population  
285 was mature in a given year. The size at which more than half of the population is mature changes by year,  
286 depending on recruitment dynamics and other demographic processes (Figure S17). After the survey data  
287 were split at the 50% at maturity size, time series of maturity-specific environmental stressors (Figure S18)  
288 were created as described below.

## 289 Temperature

290 Temperature is one of the key physical variables that structures the benthic ecosystem of the EBS (Mueter  
291 and Litzow, 2008). The cold pool, a mass of water <2 degrees Celsius, can act as a barrier to species  
292 interaction based on temperature preferences of different species. Snow crab are a stenothermic species,  
293 preferring cold water and juvenile snow crab in particular are rarely found outside of the cold pool (Dionne,  
294 2003). The cold pool is directly related to the winter ice extent in the Bering Sea and has varied dramatically  
295 over time as the ecosystem moves between cool and warm stanzas (e.g. 2006-2010 vs. 2014-2019; Figure 1b of  
296 the main text and Figure S19). As the cold pool changes from year to year, so does the spatial distribution  
297 of snow crab (Figure S20). The ontogenetic migration of snow crab results in crab of different sizes and  
298 maturity states experiencing different temperatures in a given year (Figure S21). The ‘temperature occupied’  
299 for different sizes of crab by year  $T_{s,y}$  was calculated here as an average of the observed bottom temperatures  
300 at the stations at which crab of a given size were captured  $t_i$ , weighted by the area-swept density of crab at  
301 a given station  $d_i$ :

$$T_{s,y} = \frac{\sum_i d_i t_i}{\sum_i d_i} \quad (16)$$

302 The resulting time series of temperatures occupied by size were then split by maturity state by identifying a  
303 cutoff beyond which half of the population was mature and aggregating the temperatures above and below  
304 the cutoff to represent immature and mature temperature occupied (Figure S22).

## 305 Predation

306 Pacific cod (*Gadus macrocephalus*) are the most important predator of snow crab based on stomach content  
307 data collected in the NMFS bottom trawl survey (Long and Livingston, 1998), with 16.5% of cod stomachs  
308 containing snow crab (Burgos et al., 2010). Crab ranging from 8-57 mm carapace width constitute 95% of the  
309 crab consumed by cod in the Bering Sea, but crab up to 106 mm carapace have been observed in cod stomachs  
310 (Burgos et al., 2010). An index of summer daily consumption (tons/day) of snow crab between 30-95mm  
311 carapace width eaten by Pacific cod in the eastern Bering Sea was developed using cod stomach content  
312 data from the survey to estimate the proportion by weight of crab in cod diets and the size composition of  
313 crab by carapace width of prey found in cod stomachs, stratified by year, survey stratum, and cod length  
314 (collection and analysis methods described in Livingston et al. 2017). Cod total consumption rate (metabolic  
315 demand) was calculated using a cod bioenergetics model (Holsman and Aydin 2015) to estimate laboratory-  
316 measured maximum consumption rates adjusted for bottom water temperatures and cod abundance-at-length  
317 measured at each haul location (following methods described in Barbeaux et al. 2020), and summed to an  
318 eastern Bering Sea ecosystem-wide total.

319 Changes in the cold pool can alter the interaction between snow crab and Pacific cod over time. Decreases  
320 in the size of the cold pool coincide with more northerly positions of the centroids of abundance of cod

(e.g. 2003 and 2018-2019; Figure S23 & Figure S24). This increased interaction coincided with increased numbers of crab consumed by cod in the last several years (Figure S3). The estimated number of cod greater than 50 cm was also near all-time highs around the period during which crab collapsed (Figure S25). However, this period of time also coincided with the appearance of the largest pseudo-cohort of snow crab ever seen in the Bering Sea. Given the generalist nature of Pacific cod, one would expect to see an increase in the amount of crab consumed by cod during this period of time even if there weren't differences in the interactions between the species as a result of changes in the cold pool or increases in abundance of large cod. To evaluate the possibility cod consumption has influenced the mortality of snow crab over time, the relative impact of consumption with respect to the population size must be considered. Predation indices were calculated for crab by year  $P_{m,y}$  by calculating the ratio of the extrapolated biomass of crab consumed by cod to the estimated biomass of crab,  $N_{y,m,s} * w_s$ :

$$P_{m,y} = \frac{cod_{y,m}}{\sum_s N_{y,m,s} * w_s} \quad (17)$$

The exact amount of crab eaten cannot be calculated from the available diet data because they are a snapshot of consumption at one point during the year and consumption would be expected to change with spatial overlap and temperature-driven changes in metabolism occurring throughout the year. Consequently, removals due to predation cannot be directly incorporated into the model as fishery removals might be. The index of consumption described above incorporates the most available data on cod predation, but some strong assumptions are made (e.g. summer diet is representative of the entire year). As a sensitivity to these assumptions, we also tested the ratio of the number of cod greater than 50 cm to crab abundance in a given year as an alternative index of predation in the GAMs. Ultimately, changing the index of predation did not impact the results of the fitting of the GAMs; temperature and mature population size were still the only significant covariates and the estimated shapes of relationships and deviance explained were very similar between models with the different predation indices. Consequently, the models presented in the main text use the index of consumption as the predation index because it uses the most available information on cod predation (i.e. stomach contents and the abundance and size composition of cod).

## 345 Disease

Bitter crab syndrome is a fatal disease in snow crab caused by a parasitic dinoflagellate (Meyers et al. 1996). The presence of disease is recorded in the NMFS summer trawl survey data for the subset of crab that are individually measured based on a visual inspection. Diseased crab are visually detected by a pink-orange discoloration of the carapace and opaque hemolymph. The spatial distribution of bitter crab disease is predominantly on the northeastern shelf where smaller immature animals are found (Figure S26). For this analysis, disease prevalence was calculated simply as the number of infected individuals identified in the survey divided by the total number of individuals caught in the survey for the respective maturity states (Figure S18).

## 354 Cannibalism

Cannibalism has been proposed as a potential driver of the dynamics of snow crab in eastern Canada (Lovrich et al., 1997). In laboratory studies, crab smaller than 55 mm carapace width were at high risk of being cannibalized when housed with larger crab (Lovrich et al., 1997). Crab larger than 55 mm carapace width were much less likely to be cannibalized, but the frequency of injury could be high. Here we developed an index of cannibalism based on two aspects of the spatial distribution of snow crab: the overlap of crab smaller than 55 mm carapace width with crab larger than 95 mm carapace width (Figure S27) and the density of crab larger than 95 mm carapace width within that area represents the potential 'intensity' of cannibalism in the shared area. We calculated an index of cannibalism over time as the product of exposure and intensity. Consequently, a scenario in which there was large overlap, but low densities of large crab

would result in a low cannibalism index value. Similarly, a scenario in which there was low overlap, but high densities would result in a low cannibalism index value. This produces an index that is comparable with estimated mortality—a higher cannibalism index would be expected to be associated with higher mortality if cannibalism is a strong driver of mortality in the size ranges of crab modeled here.

The proportion of smaller than 55 mm carapace width crab overlapping with larger than 95 mm carapace width crab was calculated by finding the intersection of the station IDs at which at least one crab of both size classes was observed. The density of crab larger than 95 mm carapace width was calculated as the number of >95 mm carapace width crab observed at those stations multiplied by the area swept. This exercise was also done by 5 mm size bins to show the overlap of small crab of different sizes with large crab (Figure S28). The final index aggregated all crab smaller than 55 mm carapace width (Figure S29). Indices of cannibalism were only included in the immature models given laboratory observations indicate cannibalism is rare among crab of similar sizes, though molting crab can be vulnerable.

### **Fisheries data**

Snow crab are caught both in a directed fishery (i.e. a fishery aimed at capturing snow crab) and non-directed fisheries (i.e. fisheries with targets other than snow crab). In the directed fishery, under-sized and/or dirty shelled male crab are often discarded and all females are discarded. Snow crab are discarded from non-directed fisheries using a variety of gear types (including trawl, pots, hook-and-line) and targeting a variety of species (e.g. Pacific cod, walleye pollock, and yellowfin sole) that operate over a wide fraction of the Bering Sea shelf (Figure S30). Figure S30 is plotted in log space, so it appears that the bycatch is spread widely over the shelf, but in normal space, the bycatch is more concentrated (e.g. Figure S31). The location of the centroids of the bycatch have moved over time and increases in latitude correspond with warm years in which reduced ice extent allowed for fishing farther north (Figure S32). Bycatch in trawl fisheries are by far the largest sources of bycatch mortality (Figure S33). Data on discards and bycatch of snow crab are collected by at-sea observers on fishing boats and the percent observer coverage ranges from 10% to 100%, depending on the fishery. Some fraction of the mortality imposed by non-directed fleets is likely unobserved due to crab being struck by the gear and not captured. Consequently, indices of the relative mortality imposed by fisheries discards and bycatch were calculated here as the ratio of the observed numbers of crab discarded or bycaught in a given year divided by the estimated population numbers in a given year. Only discard mortality is considered for the directed fishery in our models because the range of sizes modeled exclude the largest males, which are the targets of the commercial fishery for snow crab.

### **Crab density**

The numbers of crab estimated from the population dynamics models were also used as covariates in the GAMs. Changing densities of crab could capture aspects of intraspecific competition not captured in other covariates. Each respective model of mortality incorporates the population size of the corresponding maturity state given their spatial co-occurrence. Immature mortality also incorporates mature population size because crab are thought to move more extensively after maturing in the pursuit of mates, which suggests that their overlap with the immature portion of the population could be larger than the snapshot the survey provides. This increased overlap could result in impacts on mortality, hence the inclusion of mature population size in the immature mortality models.

### **Generalized additive models**

Generalized additive models (GAMs) were used in the R programming language (package mgcv; Wood, 2011) to relate changes in estimated mortality by maturity state and year,  $m_{m,y}$ , to environmental covariates by maturity state and year,  $\phi_{m,y}$ , because of their flexibility in fitting potential non-linear relationships. Models were first fitted in which all potential relevant covariates were included in the model of the form:

$$m_{p,y} = s(\phi_{m,y}) + \epsilon_i \quad (18)$$

410 where ‘ $s()$ ’ is a smoothing function based on thin-plate splines,  $\phi$  is a matrix of environmental covariates  
 411 scaled to mean 0 and standard deviation 1, and  $\epsilon$  is normally distributed error. The number of knots allowed  
 412 in the thin-plate splines were restricted to 3 given the relatively short time series and number of potential  
 413 stressors. Significance of covariates for the full models can be seen in Table S1 and Table S2 and the resulting  
 414 smooths in Figure S34 and Figure S35. Model diagnostics were acceptable given relatively short time series  
 415 (Figure S36 & Figure S37). Leave-one out cross validation was performed for the models by systematically  
 416 excluding a year of data, refitting the model, and recording the deviance explained and significance of the  
 417 covariates. The consistent significance of specific covariates in this exercise lends some credence that those  
 418 covariates’ influence in the model was not the result of outliers (Figure 2e). Some collinearity existed among  
 419 covariates (Figure S38 & Figure S39), but none of the collinear variables were significant in the models.

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	0.6198	0.0451	13.7414	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
$s(\text{temperature})$	2.1378	2.5245	4.7219	0.0169
$s(\text{disease})$	1.0000	1.0000	3.1106	0.0931
$s(\text{discard})$	1.0000	1.0000	0.7423	0.3991
$s(\text{bycatch})$	1.0000	1.0000	1.0154	0.3256
$s(\text{mat\_pop})$	1.8350	1.9593	4.1602	0.0252
$s(\text{predation})$	1.0000	1.0000	2.7661	0.1119

Table S1: GAM output for full model predicting mature mortality. Deviance explained = 71.32 %

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	0.1741	0.0107	16.3429	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
$s(\text{disease})$	1.0000	1.0000	0.7417	0.4004
$s(\text{temperature})$	1.8755	1.9825	11.4119	0.0005
$s(\text{mat\_pop})$	2.0000	2.0000	12.6704	0.0004
$s(\text{imm\_pop})$	1.6270	1.8596	1.7683	0.1424
$s(\text{predation})$	1.0000	1.0000	0.6671	0.4247
$s(\text{bycatch})$	1.0000	1.0000	0.0050	0.9445
$s(\text{cannibalism})$	1.7533	1.9368	2.8501	0.1134

Table S2: GAM output for full model predicting immature mortality. Deviance explained = 78.43 %

420 Models that excluded insignificant variables from each full model were used in out-of-sample prediction and  
 421 randomization tests (see Table S3 & Table S4 for covariate significance and deviance explained and Figure S40  
 422 & Figure S41 for model diagnostics). One thousand iterations of a randomization test were performed in  
 423 which the covariate time series were randomized, the models refit, and the deviance explained recorded.  
 424 This test was aimed at understanding if the explanatory power of the model was a result of the number of  
 425 covariates considered and the flexibility of the model or if the results were an indication of some underlying  
 426 signal in the data. If the deviance explained by the model using the non-randomized data exceeded the  
 427 95th quantile of the randomization trials, the deviance explained from the fitted model is less likely to be  
 428 a result of over-fitting resulting from too many covariates or too flexible smooths. The deviance explained  
 429 from both of the trimmed models exceeded the 95th quantile of deviance explained from the randomization  
 430 (Figure S42 & Figure S43). Out-of-sample predictions were made by excluding the last 1,2, and 3 years of  
 431 data, refitting the model, then attempting to predict the held out data based on the covariates observed in  
 432 those years (see figure 2 of the main text for a discussion and Figure S44 for a larger version of figure 2).

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	0.6198	0.0481	12.8854	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(temperature)	1.8741	2.2587	4.2891	0.0246
s(mat_pop)	1.8497	1.9631	6.7637	0.0036

Table S3: GAM output for trimmed model predicting mature mortality. Deviance explained = 60.46 %

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	0.1741	0.0125	13.9569	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(temperature)	1.7403	1.9315	9.3351	0.0007
s(mat_pop)	1.9803	1.9985	6.6509	0.0056

Table S4: GAM output for trimmed model predicting immature mortality. Deviance explained = 59.53 %

### 433 Sensitivities to model assumptions in GAMs

434 Modeling decisions are also necessarily made in the process of fitting GAMs and it is possible for these  
 435 decisions to influence the outcome of an analysis. Within the context of our model, these decisions include  
 436 the assumed error structure, the treatment of the uncertainty associated with the estimates of mortality, and  
 437 the allowed shape of the smooths estimated in the GAMs. The following sensitivities address the implications  
 438 of these modeling decisions on the outcome of our analysis.

#### 439 Error structure

440 Impacts of assumptions about error structure were explored by assuming beta distributed data in the GAM  
 441 and transforming the continuous total mortality rates to an exploitation rate ranging from 0 to 1. This  
 442 transformation still resulted in mature population and temperature being the most important variables  
 443 related to mortality, however the deviance explained decreased to 58% and 70% for mature and immature  
 444 mortality, respectively, compared to 71% and 78% for the model presented in the main text. A potential  
 445 shortcoming of the method presented in the main text is that predicted mortality could be less than zero.  
 446 This was not the case in any of the model fittings, and would present a problem primarily if the model was  
 447 extrapolated to data beyond the observed ranges. A potential fix to this issue is to log the response variable,  
 448 but this resulted in unacceptable patterns in the residuals, so this model was not used.

#### 449 Does incorporating the uncertainty in the estimates of mortality change analysis outcomes?

450 The models presented in the main text use the maximum likelihood estimates of mortality from the popu-  
 451 lation dynamics models as response variables in the GAMs. However, each of those estimates of mortality  
 452 have associated uncertainty estimated in the fitting process. One way of evaluating the impact of incorpo-  
 453 rating the estimated uncertainty from the population dynamics model into the GAM fitting process can be  
 454 accomplished in 4 steps:

- 455 1. Invert the Hessian matrix produced from fitting the population dynamics model to calculate a covari-  
 ance matrix describing the relationships between each of the estimates of mortality,
- 456 2. Simulate time series of the estimated mortality from a multivariate normal distribution with a mean  
 of the point estimates of mortality deviations and the product of step 1 as the covariance matrix,
- 457 3. Refit the GAMs to these simulated mortality time series and record the deviance explained and p-values  
 for each covariate,
- 458 4. Repeat these steps many times.

462 A similar methodology can be seen in Johnson et al. (2022). Each of these steps were taken in the R  
463 programming language. Inverting the Hessian was accomplished by using the function ‘solve()’; simulating a  
464 time series of mortality deviations was accomplished using the function ‘mvrnorm()’. The resulting simulated  
465 time series of mortality were very similar to the maximum likelihood estimates of mature and immature  
466 mortality, reflecting relatively precise estimates of mortality (Figure S45). The deviance explained across  
467 simulated time series were also similar to that produced with the MLE time-series of mortality. Temperature  
468 and mature population remained the most important variables in predicting mortality across GAMs fitted  
469 to simulated time-series of mortality (Figure S46). Given this outcome, the model presented in the main  
470 text does not consider the uncertainty associated with treating the estimates of mortality as ‘data’ in the  
471 fitting of the GAMs.

#### 472 **Shape of estimated relationships**

473 The model presented in the main text constrains the number of knots available to the GAM to fit the data for  
474 each covariate to 3, but the shapes of GAM-estimated smooths are not constrained. This modeling choice was  
475 made because it is not immediately clear a priori what the shape of the smooths should be. For example,  
476 the relationship between immature population size and immature mortality could conceivably be linear  
477 positive (e.g. higher populations result in higher mortality due to intraspecific competition), linear negative  
478 (e.g. larger population sizes dilute the impact of external stressors like predation and fishery effects), dome-  
479 shaped (somewhat harder to interpret, but perhaps different processes are important at different population  
480 sizes), or monotonic in either direction (e.g. population size modulates external stressors to a point, after  
481 which other processes are more important).

482 The model in the main text is unconstrained with respect to the shape of the estimated relationships between  
483 mortality and covariates. However, the relationship between immature mortality and mature population size  
484 was markedly dome-shaped and a satisfying biological explanation for this shape is not immediately appar-  
485 ent. To explore the impacts of unconstrained estimation of this relationship, we refit the models using shape  
486 constrained additive models in the R package ‘scam’ (based on Pya and Wood, 2015). This allows the user  
487 to specify constraints on the shape of relationships between model variables (e.g. monotonically increasing  
488 or decreasing). We refit our model for immature mortality with the assumption that the relationship be-  
489 tween immature mortality and mature population size can only be monotonically increasing (similar to the  
490 estimated relationship between mature mortality and mature population size). The rest of the covariates  
491 were specified as linear predictors, except temperature, which remained a non-linear smooth. Given the  
492 importance of temperature in the hypotheses we present, we were particularly interested to understand how  
493 the assumptions about the shape of other significant covariates influence the estimated relationship between  
494 temperature and mortality.

495 Temperature and mature population size were still significant covariates within the shape constrained additive  
496 model and immature population size became significant (Table S5). The estimated relationship between  
497 mortality and temperature was still strongly positive, but became more linear with the shape constraints  
498 imposed on mature population size (Figure S47). The relationship between immature population size and  
499 immature mortality was negative (i.e. all other things considered, more immature crab were associated with  
500 lower mortality). While the immature population relationship is potentially interesting, the most important  
501 outcome of this exercise is that temperature still returned positive relationship with estimated mortality.  
502 Using temperature as the only covariate in an unconstrained GAM explained 37% and 38% of the deviance  
503 in immature and mature mortality (not shown). All of these points suggest temperature is a key covariate  
504 in the estimated mortality dynamics for snow crab in the eastern Bering Sea.

#### 505 **How could temperature relate to mortality mechanistically?**

506 Increased temperature was consistently correlated with increased estimated mortality in our models, but the  
507 range of temperatures observed were not beyond the thermal tolerances of snow crab. Foyle et al. (1989)  
508 captured 20 snow crab of carapace size 85–95 mm in 1986 and raised them in the lab in a range of thermal  
509 regimes to understand the impacts of increased temperatures on mortality and caloric requirements for snow

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-0.0325	0.1850	-0.1757	0.8623
disease	0.0236	0.0162	1.4561	0.1607
imm_pop	-0.0374	0.0174	-2.1454	0.0442
predation	0.0002	0.0169	0.0137	0.9892
bycatch	-0.0003	0.0147	-0.0194	0.9847
cannibalism	-0.0090	0.0153	-0.5887	0.5626
B. smooth terms	edf	Ref.df	F-value	p-value
s(temperature)	1.0005	1.0009	6.7766	0.0167
s(mat_pop)	1.7664	2.0738	3.5320	0.0466

Table S5: GAM output for a shape constrained model predicting immature mortality. Deviance explained = 59.53 %

510 crab. In addition to identifying the thermal tolerances of snow crab (crab stop eating around 12 degrees  
 511 C), Foyle et al. observed a doubling of caloric requirements for snow crab held in 3 degrees Celsius water  
 512 as compared to those in 0 degree waters. Here we calculated an index of the caloric requirements for the  
 513 modeled fraction of the population of snow crab in the eastern Bering Sea over time using the abundance  
 514 at size of snow crab observed in the NMFS survey, the temperature occupied of crab at size calculated from  
 515 observations of bottom temperature in the NFMS survey, and the observations of caloric requirements of  
 516 snow crab by temperature produced by Foyle et al. (1989). The relationship between temperature and the  
 517 caloric requirements of snow crab ( $kCal_t$ ) reported by Foyle et al. was:

$$kCal_{s=90mm,t} = 2.2 * e^{\frac{-(t-5.2)^2}{30.7}} \quad (19)$$

518 Snow crab numbers at size (s) by year (y) ( $N_{s,y}$ ) and the temperature occupied at size by year ( $T_{s,y}$ ) were  
 519 calculated as described above. The caloric requirements reported in Foyle et al. were based on observations  
 520 of crab that were 85-95 mm carapace width, so these results need to be extrapolated to the range of sizes  
 521 used in this analysis. Kleiber's law (Kleiber, 1947) states there is a consistent relationship between the body  
 522 mass and metabolic requirements of organisms (kCal). The relationship has been generalized as:

$$kCal_m = mass^{0.75} \quad (20)$$

523 Calculating the metabolic requirements for snow crab at size by year,  $kCal_{s,y}^{snow}$ , can be calculated by  
 524 evaluating the caloric requirements of 90mm carapace width crab at a given temperature were calculated,  
 525 then scaling that up or down based on Kleiber's law:

$$kCal_{s,y}^{snow} = \frac{2.2 * e^{\frac{-(t-5.2)^2}{30.7}}}{300^{0.75}} w_s^{0.75} \quad (21)$$

526 Caloric requirements increased sharply in 2018 and to explore potential impacts of this increase, we analyzed  
 527 the weight at size data available (Figure S48). A GAM was used to predict observed weights at size  $w_{i,s,y}$   
 528 using the bottom temperature in which the crab was collected,  $t_i$ , measured carapace width  $cw_i$ , and year  
 529 as a factor:

$$w_{i,s,y} = s(cw_i) + s(t_i) + year + \epsilon \quad (22)$$

530 The GAM explained 97.4% of the deviance in the weights of snow crab and all covariates were significant  
 531 (Table S6).

532 In general, higher temperatures were associated with higher weight at size (Figure S49). The weight at size  
 533 curves for 2015 and 2017 were scaled significantly higher than the base year of 2011, whereas the year 2018

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	218.5199	2.2252	98.2019	< 0.0001
as.factor(AKFIN_SURVEY_YEAR)2015	6.4525	3.1690	2.0361	0.0419
as.factor(AKFIN_SURVEY_YEAR)2017	12.6093	2.4840	5.0763	< 0.0001
as.factor(AKFIN_SURVEY_YEAR)2018	-11.9217	6.2536	-1.9064	0.0568
as.factor(AKFIN_SURVEY_YEAR)2019	4.0886	2.7473	1.4882	0.1369
B. smooth terms	edf	Ref.df	F-value	p-value
s(WIDTH)	6.4225	7.5862	6340.9617	< 0.0001
s(GEAR_TEMPERATURE)	1.9362	2.3359	17.0800	< 0.0001

Table S6: GAM output for model predicting male snow crab weight. Deviance explained = 97.4%

534 was marginally significantly lower ( $p=0.057$ ). The marginal significance likely resulted from the relatively  
 535 small sample size of weight at size available in 2018 ( $N=27$ ), but the effect size was large (the coefficient  
 536 associated with 2017 was 12.60; the coefficient associated with 2018 was -11.92) which translated to large  
 537 differences in estimated weight at size between the years reported in the main document. Previous studies  
 538 looking at the impacts of starvation on the weight at size of snow crab (e.g. Hardy et al., 2000) reported small  
 539 changes in weight at size (roughly 2.6% of weight lost over 5 months), but larger changes in the weight of the  
 540 hepatopancreas. However, there are some key differences between these studies and the field observations  
 541 we report. First, the maximum observed mortality was 20% in the starvation studies; the mortality levels  
 542 estimated in the Bering Sea exceeded 90% in some years. Second, the starvation experiments were in  
 543 laboratory environments where no foraging occurred. Seventy crab were confined in containers measuring  
 544 122 x 183 x 40 cm in Hardy et al. (2000), which greatly restricted movement and would presumably impact  
 545 caloric expenditure and the initiation of catabolism of muscle tissue.

## 546 A word on methods

547 Attribution of changes in population processes in ecology is a difficult problem, particularly for wild pop-  
 548ulations that are difficult to directly observe and impossible to experiment on in situ. There are a large  
 549 range of methodologies that claim to identify causality in observational data (structural equation modeling,  
 550 empirical dynamic modeling, etc.). Some of the difficulties in determining causality in ecological time series  
 551 are related to the generally short time series that are available, non-linear dynamics, and departures of pop-  
 552ulations or covariates into unexplored parameter space. These issues can present problems for any modeling  
 553 framework and we have tried to address these to the best of our ability with the models used here. The use of  
 554 p-values has been (rightfully) criticized in the literature and the explanatory power of our models are likely  
 555 overstated given these criticisms. Ultimately, the numerous sensitivities and simulation tests performed here  
 556 were undertaken to try to understand if a suite of covariates appear to be important under different modeling  
 557 decisions and considerations of uncertainty, in spite of the potential short-comings of the data available and  
 558 models selected. Temperature and population density appear to be these covariates.

## 559 Frequently asked questions

### 560 Are you sure the collapse wasn't a result of cod predation?

561 The predation index (i.e. the crab consumed by cod divided by the crab available; Figure S18) was near the  
 562 time series average during the collapse in 2018 and 2019. If predation were a strong driver of the mortality  
 563 during the collapse, it is difficult to explain why estimated mortality was not high when the predation indices  
 564 were much higher in the late 1990s and mid-2010s. Furthermore, the distribution of the cod population  
 565 during 2018 and 2019 extended much farther north, beyond the portion of the snow crab population that is  
 566 included in this analysis. Movement north can happen in particularly warm years and would serve to reduce  
 567 the relative predation pressure on the portion of the population of crab in this analysis because the cod that

568 moved north would be consuming crab outside of our study area. Finally, a large fraction of the missing  
569 crab from the recent collapse were not of the sizes typically eaten by cod (Figure S50).

570 Although our predation indices incorporate the best available information about cod diet and abundance,  
571 these indices are snapshots taken during the summer survey. It is possible that the consumption of crab was  
572 different in other times of the year and, if this were true, knowing how predation changed throughout the  
573 year could alter our results.

574 **Are you sure the collapse wasn't a result of trawling?**

575 The bycatch index steadily declined since the beginning of our study, with the relative impact of trawling  
576 in 2018 and 2019 below the historical average (Figure S18). It is difficult to reconcile the idea that trawling  
577 could have contributed to the collapse with the relatively low mortality rates estimated during the periods  
578 when the bycatch index was many times higher in the 1990s. Furthermore, if trawling were a large source  
579 of mortality for snow crab, it is difficult to understand how the largest pseudocohort ever observed could  
580 have established and survived for ~8 years on the Bering Sea shelf, during which the trawling pressure was  
581 relatively consistent. It should be noted that trawling occurred farther north in 2018 than usual and some of  
582 this effort overlapped with the area in which the largest densities of crab were observed and lost (Figure S30).  
583 However, the intensity of trawling in that area and the observed bycatch of snow crab in the areas of highest  
584 density were very small compared to other areas in the Bering Sea and historical values (Figure S31).

585 Not all of the mortality associated with non-directed fleets is observed. It is possible that crab on the seafloor  
586 are impacted by the trawling gear and die as a result of their injuries. The index used in this analysis is a  
587 reliable indicator of the trend in bycatch mortality provided the ratio of observed to non-observed mortality  
588 is consistent over time. If this is not the case, that could change the outcome of our analysis, but there is  
589 no clear methodology for accurately determining that ratio.

590 **What do crab eat? If they starved, did there appear to be large declines in their prey base?**

591 Snow crab have a wide-ranging diet of bivalves, polychaetes, crustaceans, and gastropods in the northern  
592 Bering Sea (Kolts et al., 2013). They appear to be a generalist, consuming whatever they can capture and  
593 crush with their claws. Kolts et al. (2013) reported that most prey items were consumed in proportion to  
594 their estimated abundances, except polychaetes, which seemed to be preferentially selected. Indices of prey  
595 biomass can be calculated from the NMFS trawl, however the survey gear does not sample these species well.  
596 With that caveat, the average of three of the clusters of scaled prey biomass by group from the survey were  
597 below the long-term mean in 2018 and 2019 (Figure S51). While this is suggestive, these time series require  
598 further validation before placing any confidence in them and were therefore not used in the main analysis.

599 Even if these time series were reliable and there appeared to be abundant forage for snow crab in warm years,  
600 the metabolic trade-off between the energy required to obtain, handle, and digest their prey and the energy  
601 derived from prey would need to be considered when trying to understand if metabolic demands could be  
602 met. This would be a useful area of further research, particularly if reliable time series of benthic forage  
603 could be identified and maintained.

604 **If it was a large mortality event, did you see large numbers of empty carapaces in the survey?**

605 Hundreds of millions of carapaces are discarded by molting crab each year even when there are no mortality  
606 events and these are rarely seen in the survey nets. So, even with a massive mortality event, one might not  
607 expect to see the carapaces remaining from the event. Why the carapaces are not seen in the survey nets is  
608 not completely clear, but potential hypotheses include relatively fast disintegration on the sea floor or poor  
609 selectivity by the survey gear. Discarded carapaces may sit flat on the bottom and be passed over by the  
610 net.

611 **Were that many crab really in the eastern Bering Sea to begin with? Was the ‘collapse’ an  
612 artifact of some survey error?**

613 The NMFS summer survey was originally designed to estimate crab abundances (Zimmermann et al., 2009)  
614 and the recent survey methodology has been repeatedly validated as a useful tool for estimating crab abun-  
615 dance (see Somerton et al., 2013, for example). Snow crab are widely distributed on the shelf and conse-  
616 quently well sampled by the survey. There are 375 survey locations in the NMFS eastern Bering Sea trawl  
617 survey, of which 349 are on a 400 square nautical mile grid. The remaining stations are in high density  
618 sampling areas around islands in the Bering Sea implemented to better estimate crab abundances around  
619 those islands. On average, snow crab are observed at 233 of the 349 survey stations on the standard grid.  
620 In 2018 a large number of stations returned estimated high densities of crab (see Fig. 1 of main text), which  
621 means that the large estimates of abundance in 2018 were not driven by one or two large survey tows.

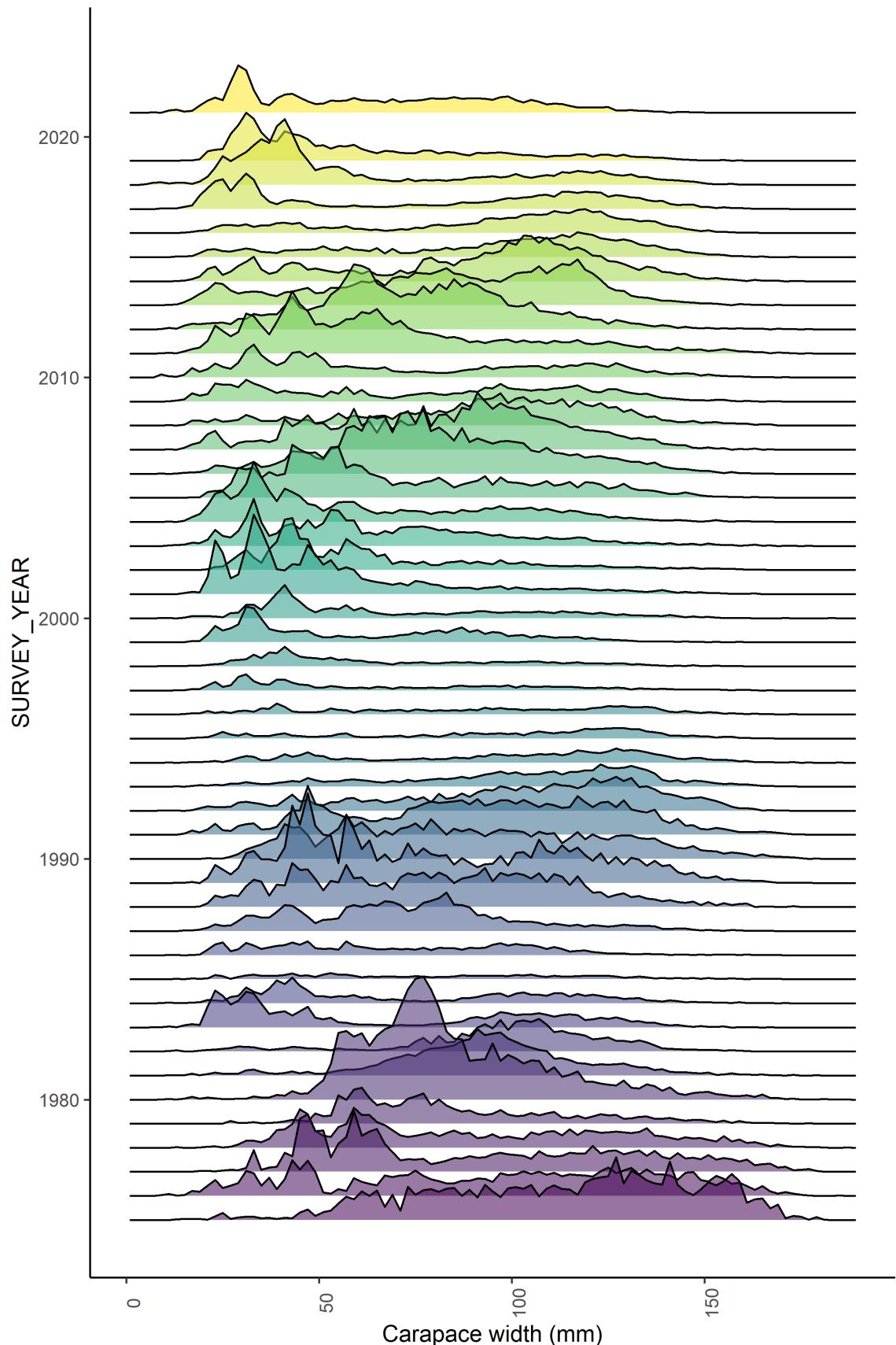


Figure S1: Observed abundance by carapace width of Tanner crab in the NMFS summer survey.  
18

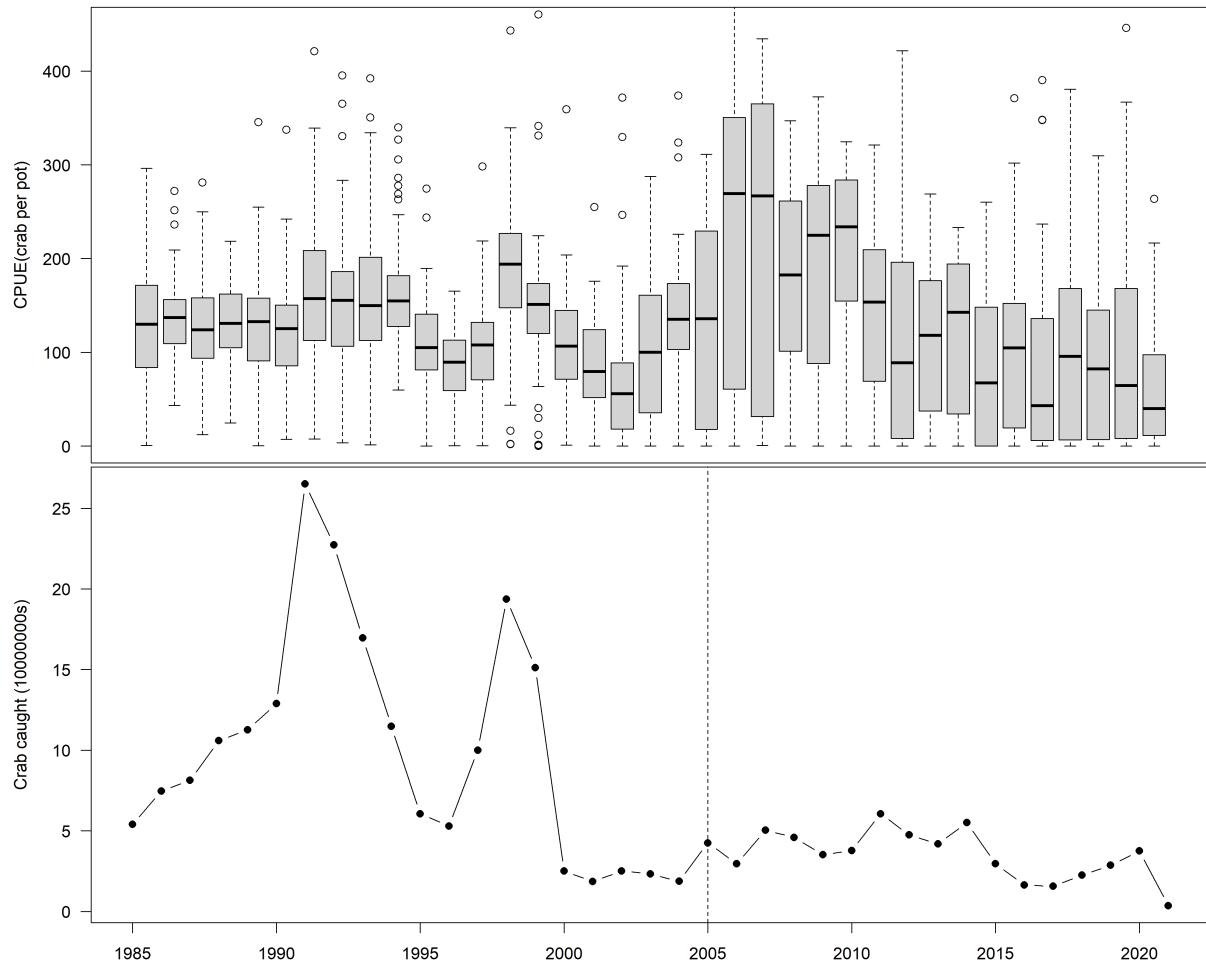


Figure S2: Fishery CPUE (top; black lines are median, grey box represents 25-75th quantiles, circles are outliers) and number of crab caught in the directed snow crab fishery (bottom). Vertical dashed line represents the introduction of individual transferrable quota management. CPUEs before and after are difficult to compare as a result of changes in fleet behavior.

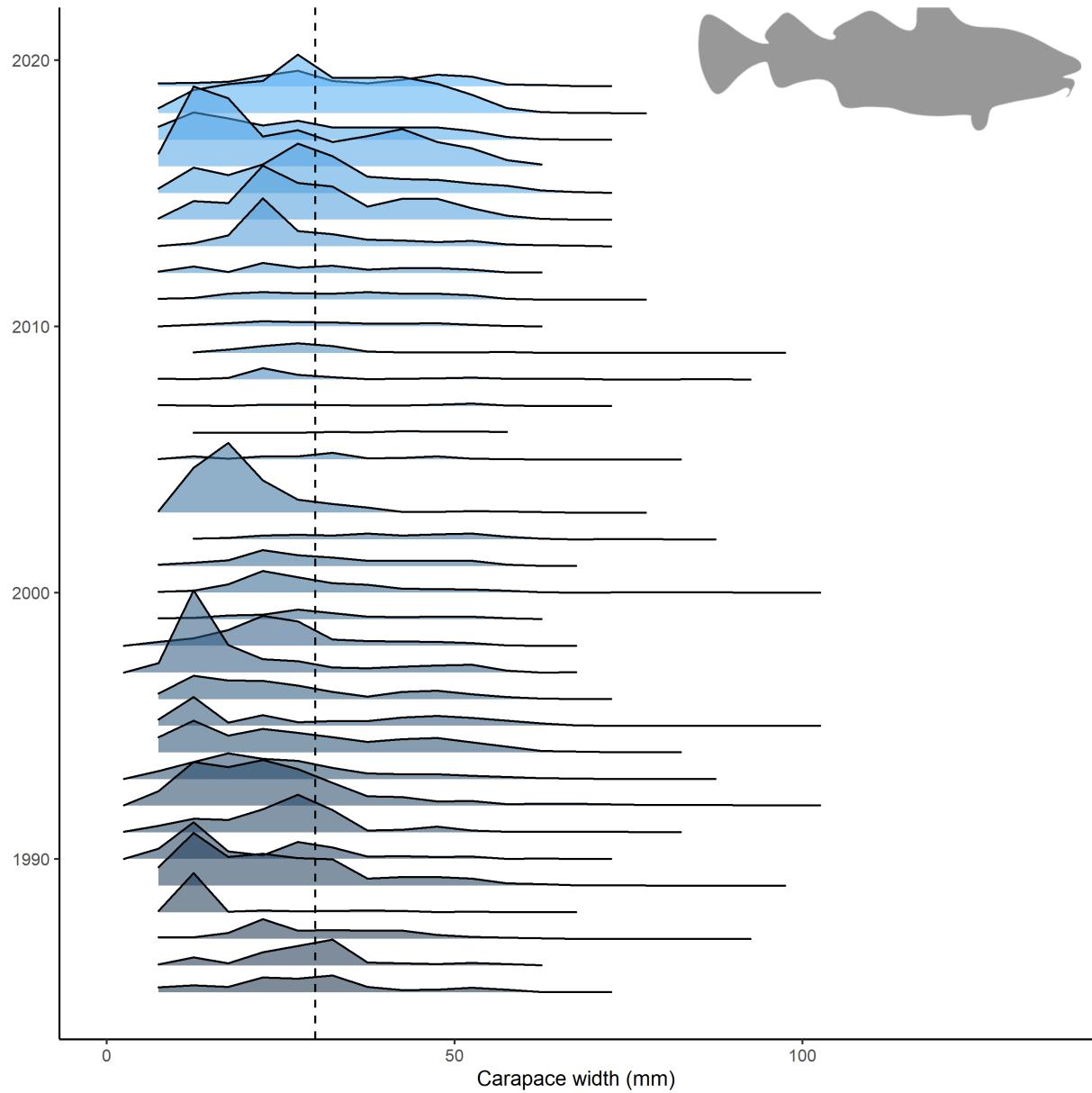


Figure S3: Consumption of crab by Pacific cod at size over time. Dashed line represents the size at which crab enter the population dynamics model presented in the text.

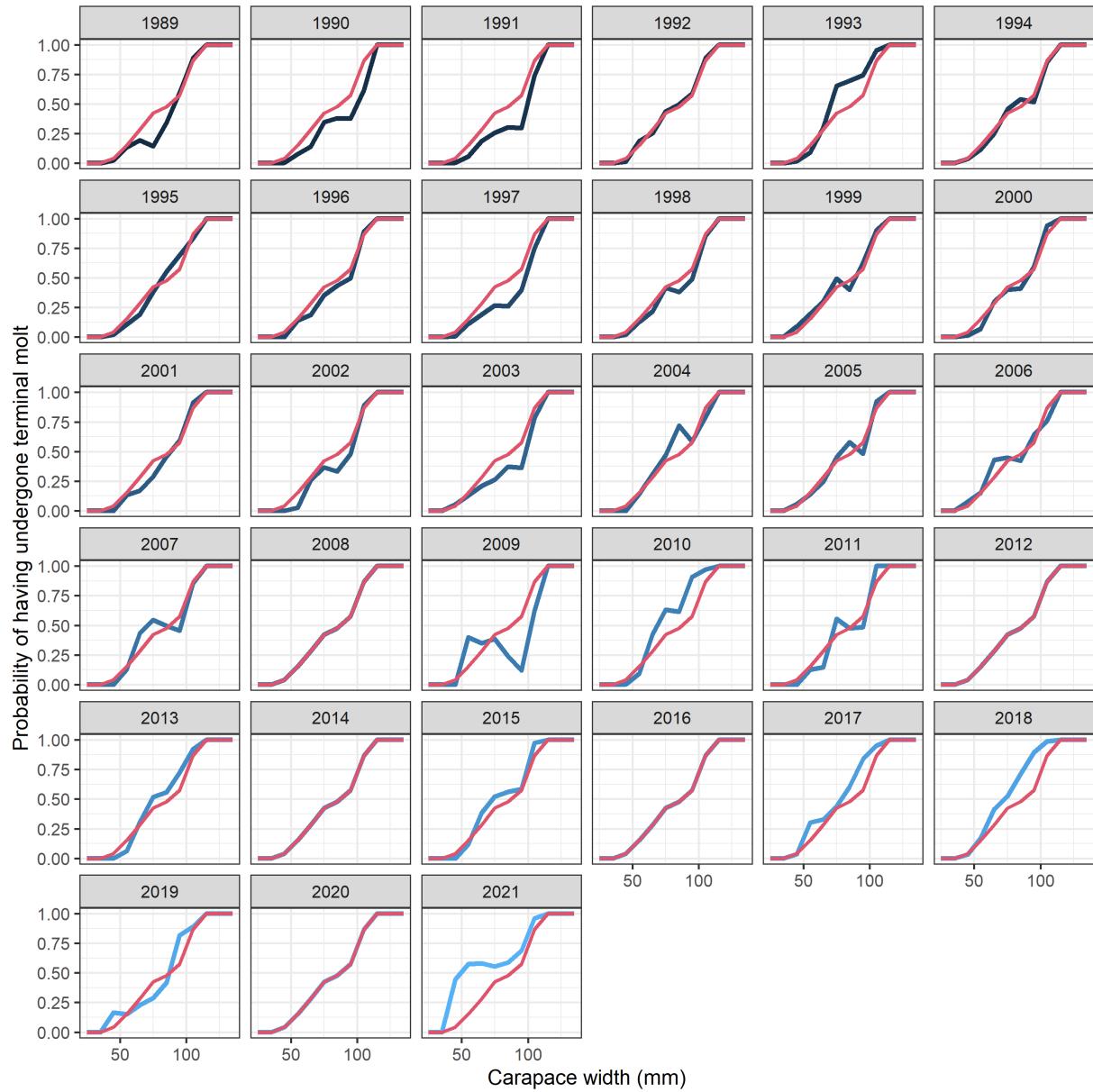


Figure S4: Observed proportion of mature new shell crab in the NMFS summer survey. Red line represents the median over years and the blue lines are the observed data. Chela height data were not collected in years without a blue line. These data are used to separate the numbers at size into mature and immature states for the input data to the population dynamics model.

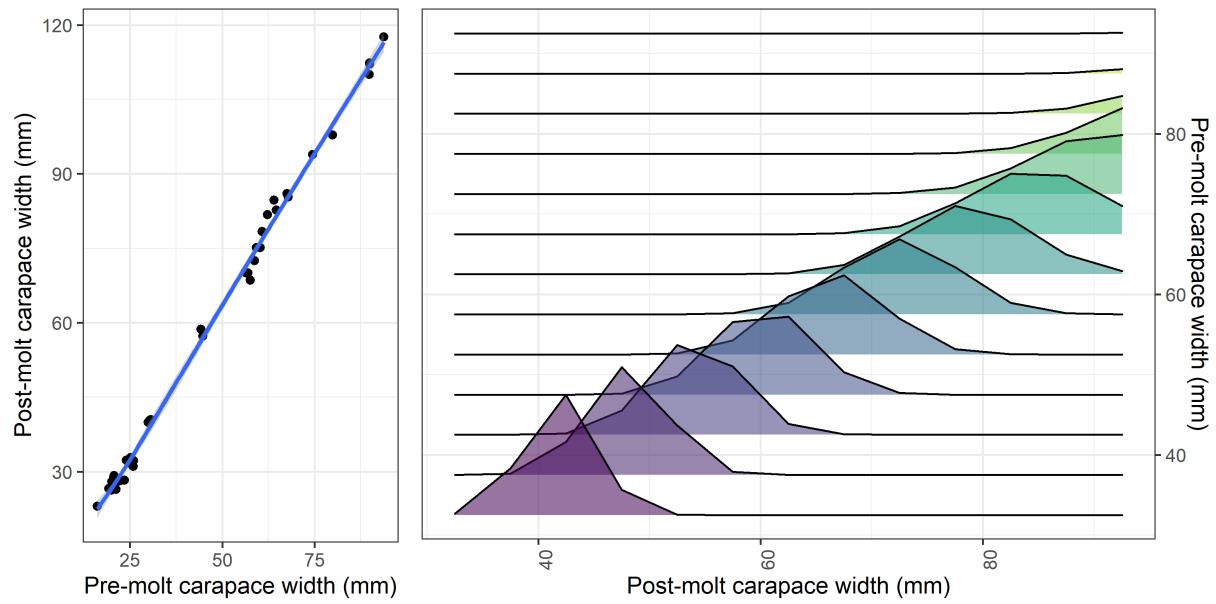


Figure S5: Empirical relationship between pre- and post-molt size (left) derived from crab captured in the wild pre-molt and observed to molt in the lab. Calculated size-transition matrix used in the population dynamics model (right).

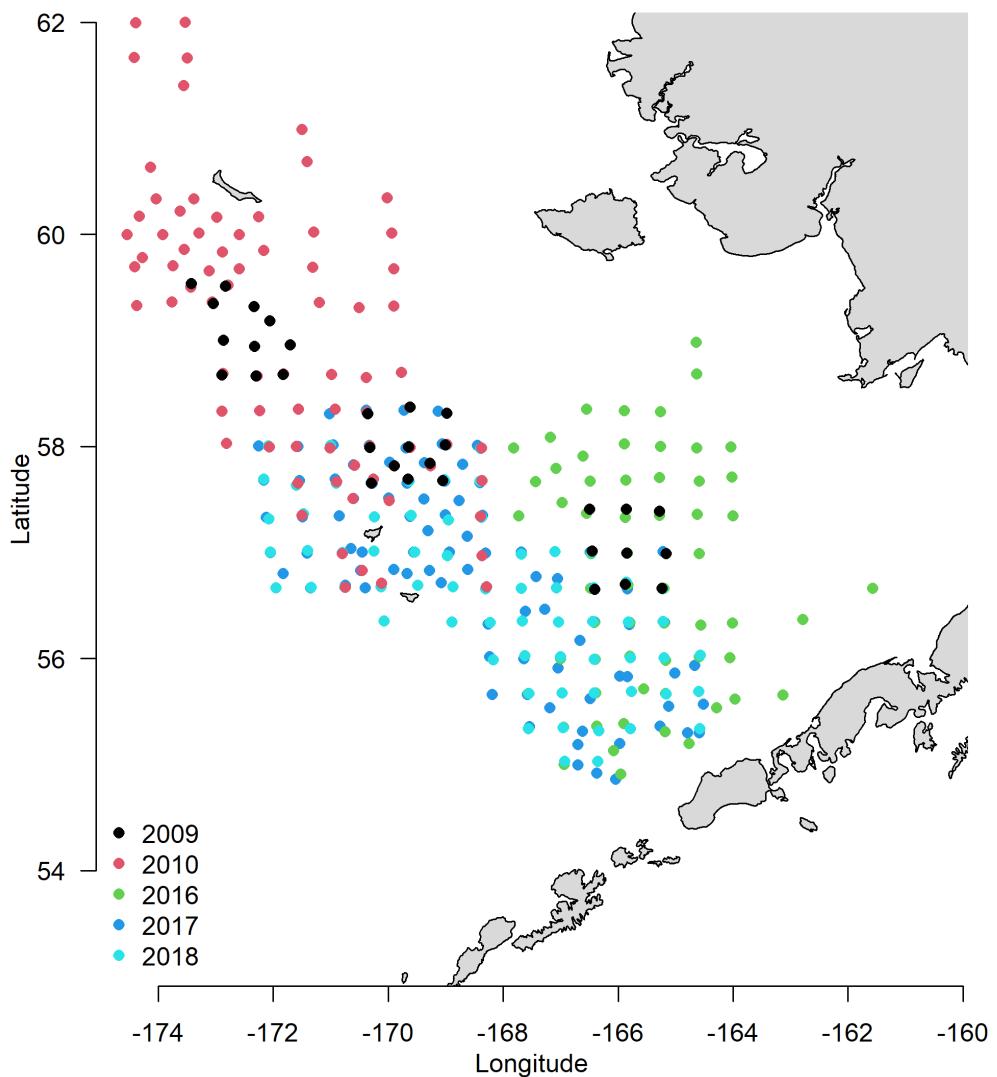


Figure S6: Locations of the BSFRF experimental trawls to evaluate the capture efficiency of the NMFS summer trawl survey for snow crab in the eastern Bering Sea.

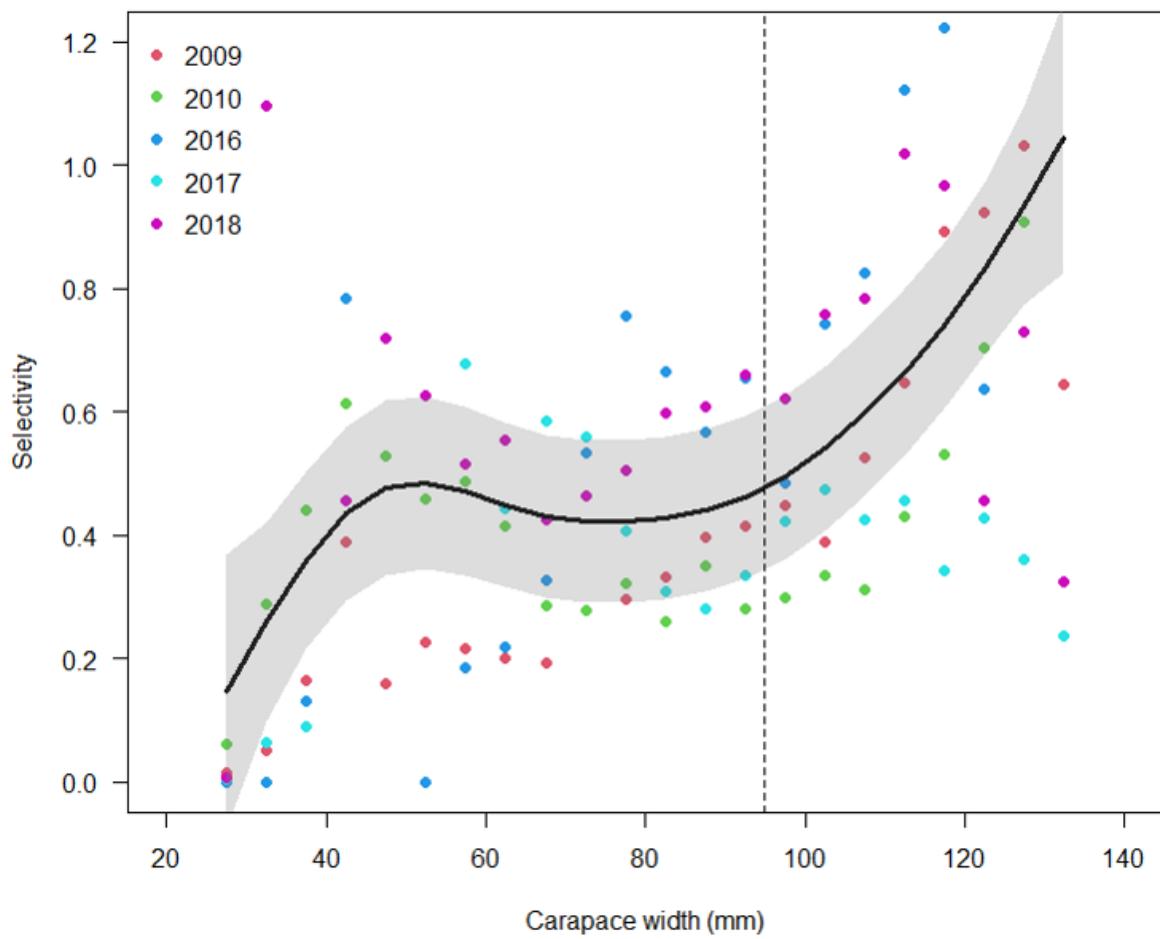


Figure S7: Inferred selectivity from the BSFRF experimental trawls.

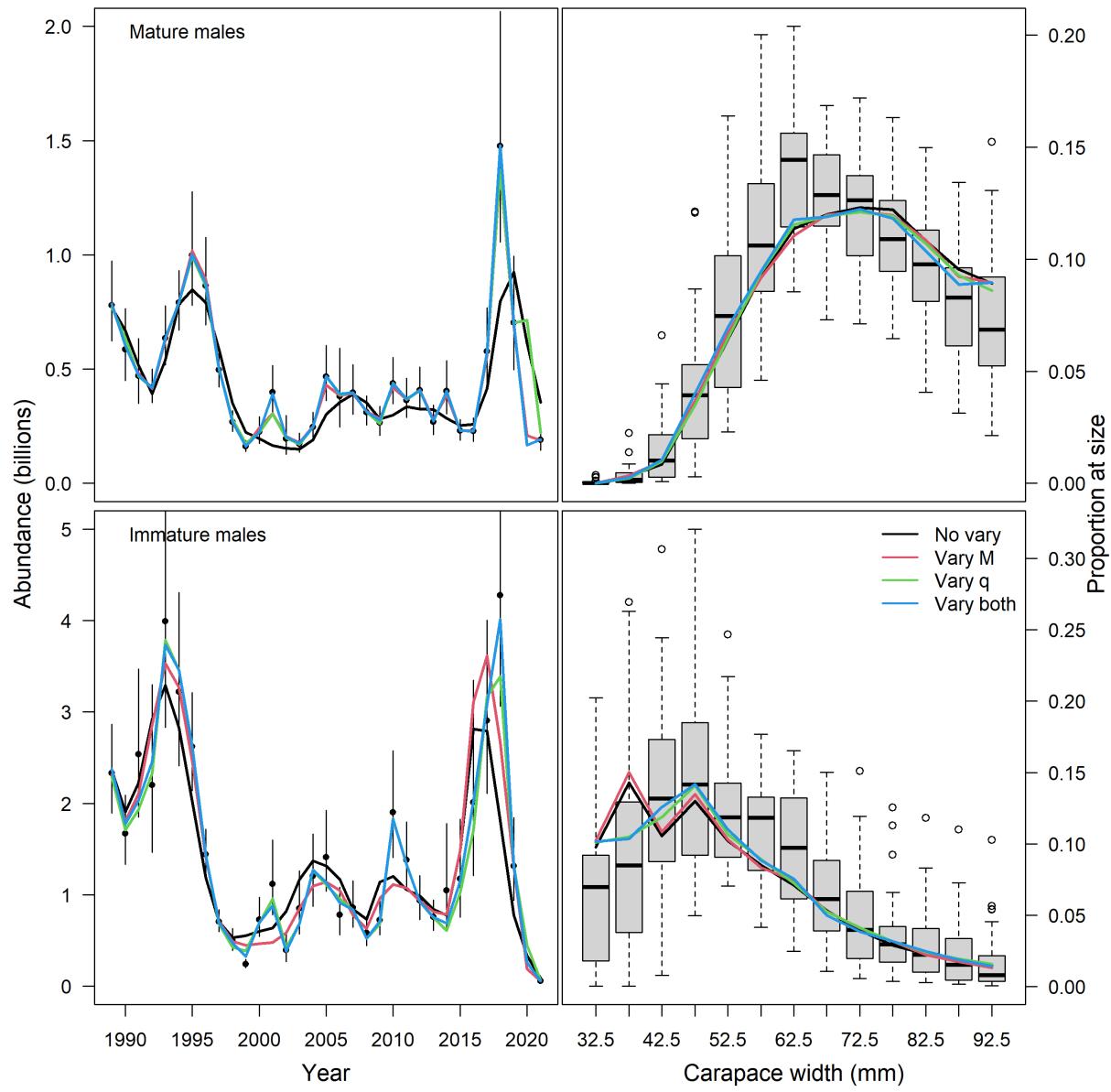


Figure S8: Fits of models with increasing complexity in mortality and catchability. Index of abundances are on the left with observations in black dots with 95% confidence intervals; colored lines are model fits. Size composition data are at the right with observations in box plots (aggregated over year; black lines are median, grey box represents 25-75th quantiles, circles are outliers) and colored lines are model fits.

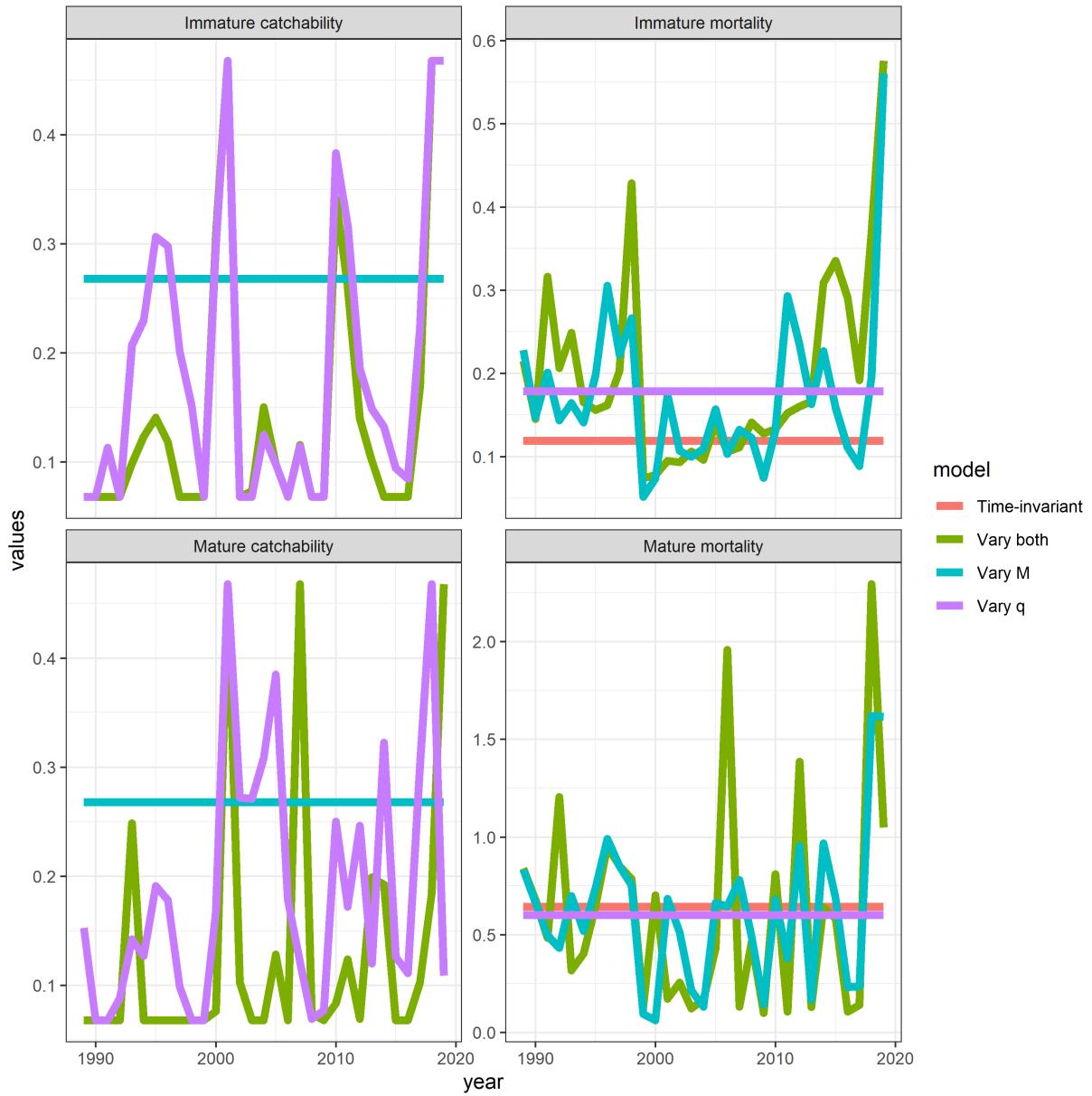


Figure S9: Estimated processes from model with increasingly complex time-variation in mortality and catchability.

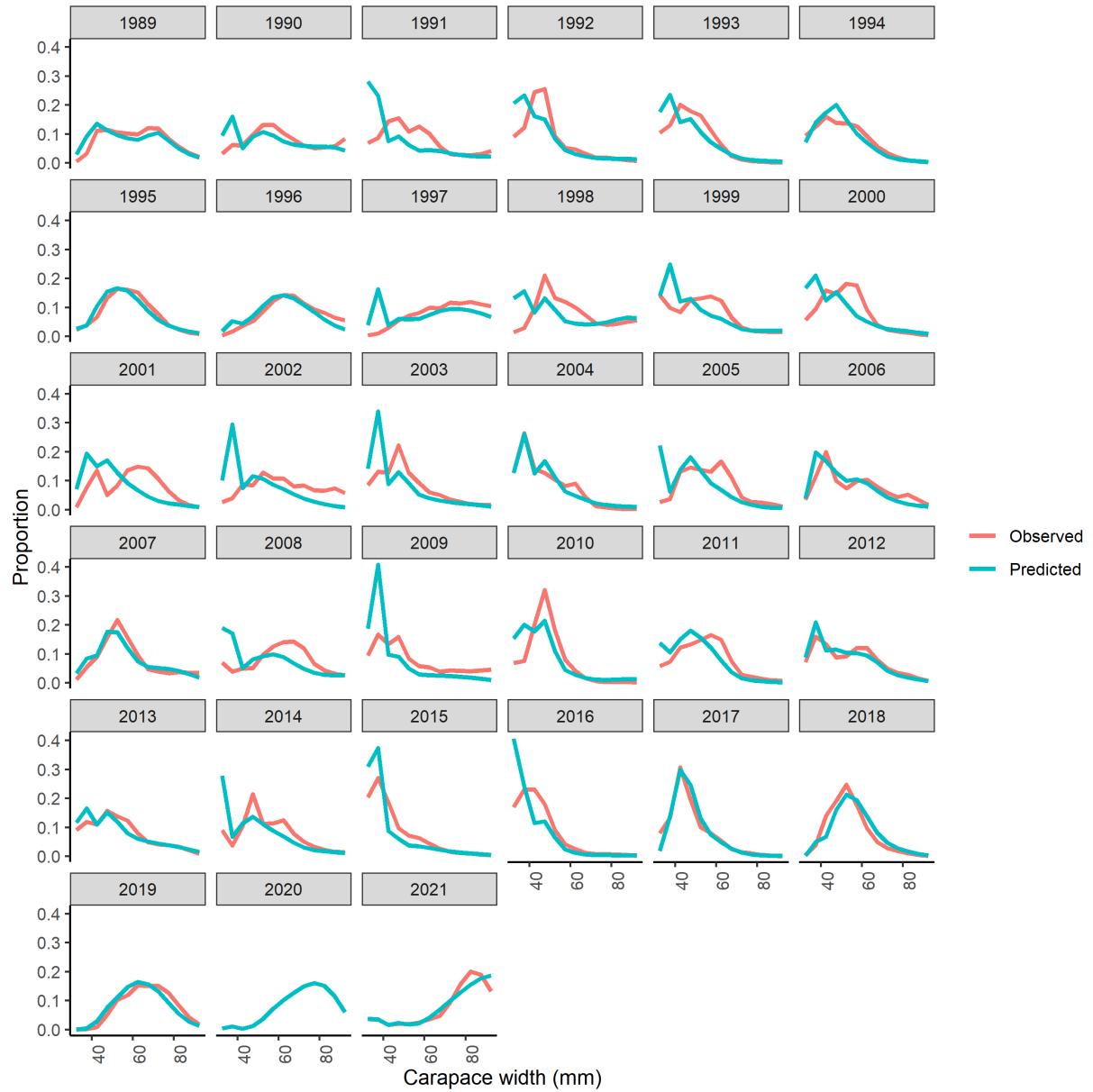


Figure S10: Fits for individual years to immature size composition data from a model in which mortality varied over time.

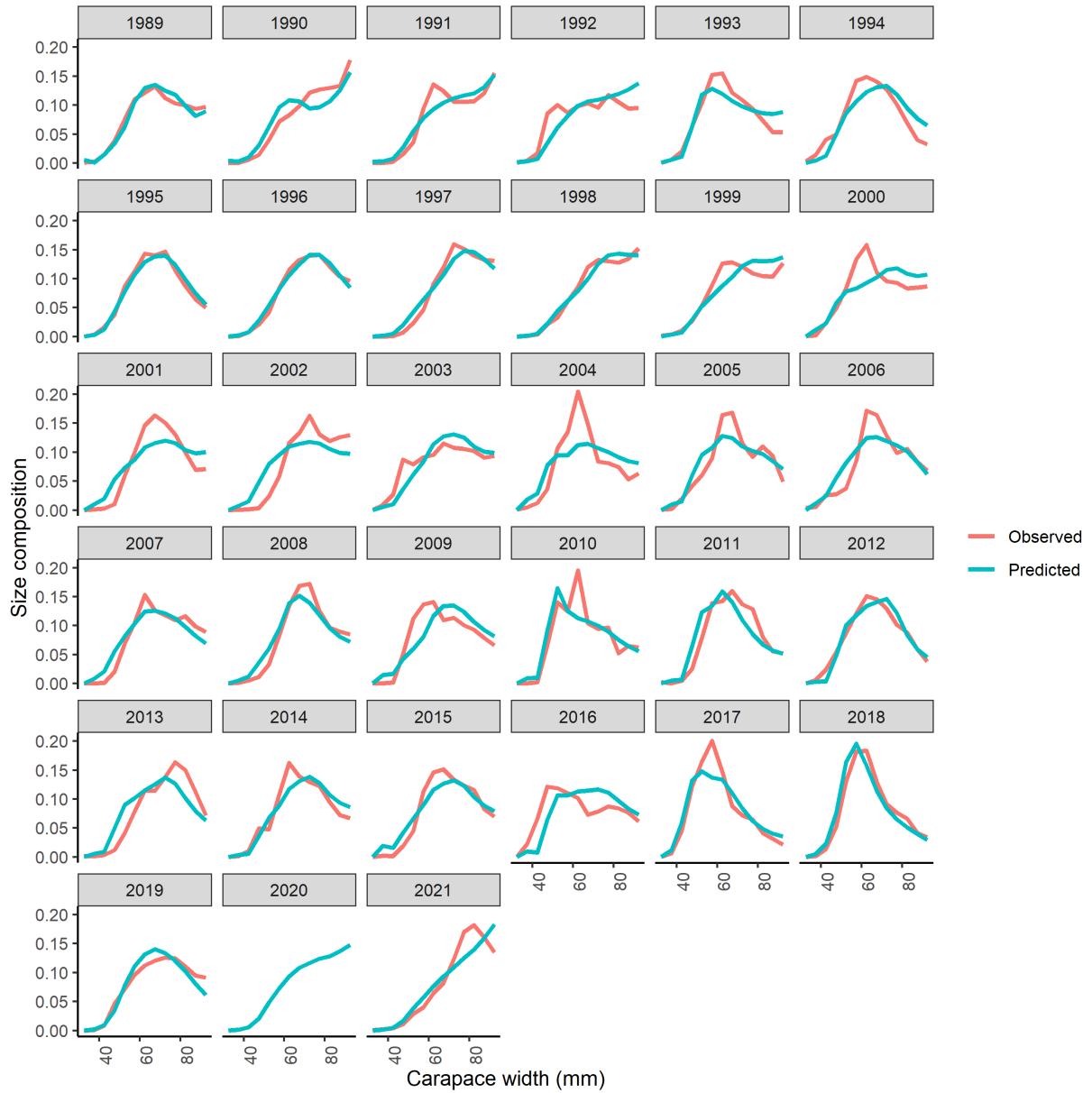


Figure S11: Fits for individual years to mature size composition data from a model in which mortality varied over time.

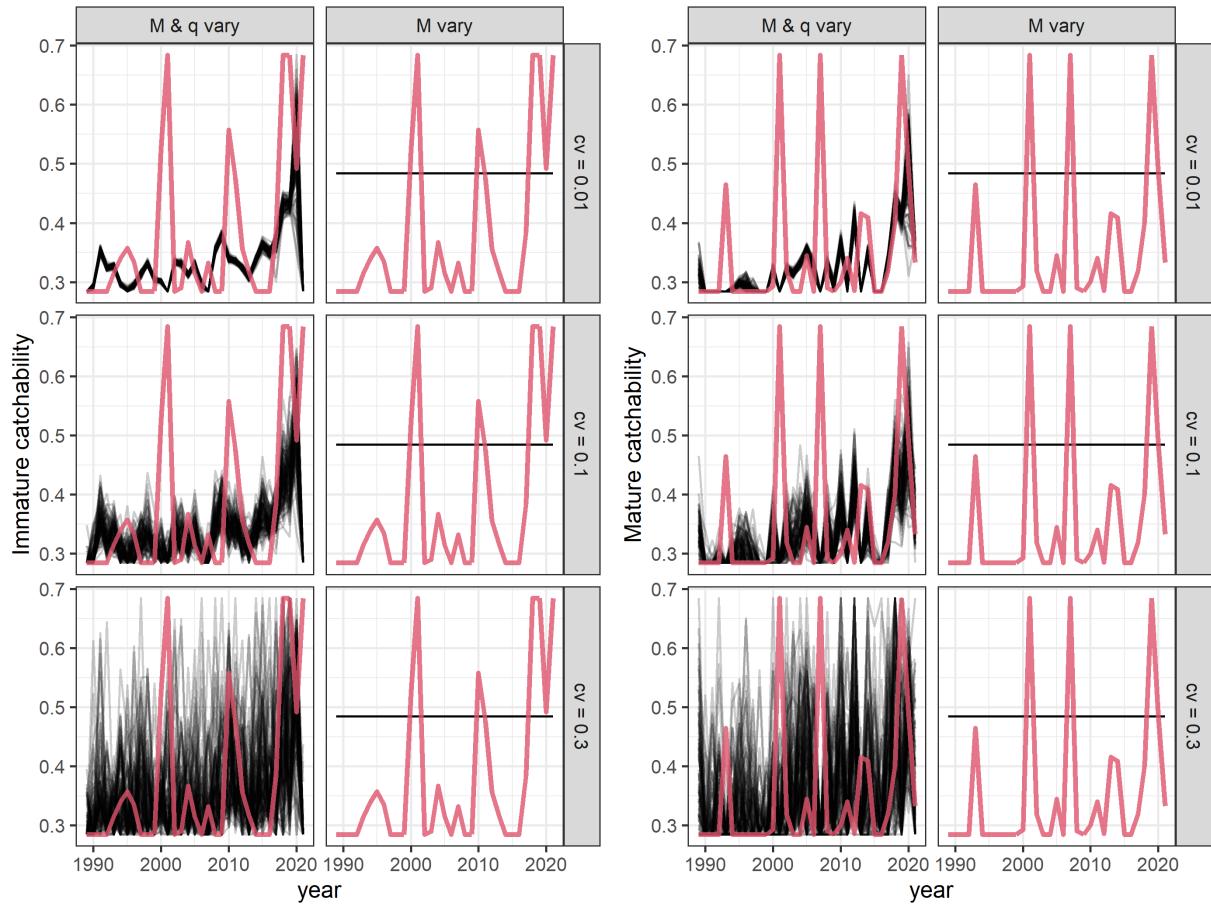


Figure S12: Estimates of catchability by maturity state (black lines) compared to the underlying values (red line) from simulations testing the estimation ability of the population dynamics models.

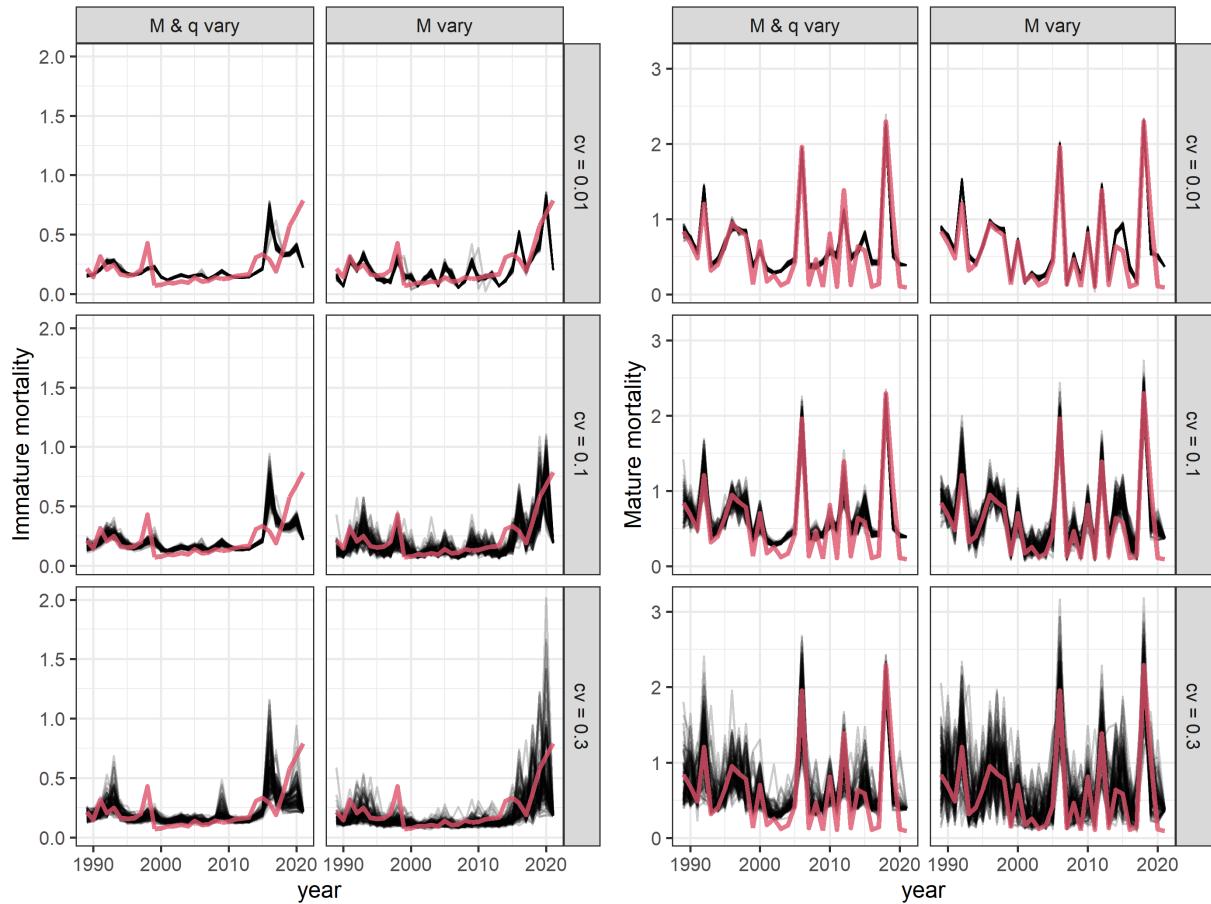


Figure S13: Estimates of mortality by maturity state (black lines) compared to the underlying values (red line) from simulations testing the estimation ability of the population dynamics models.

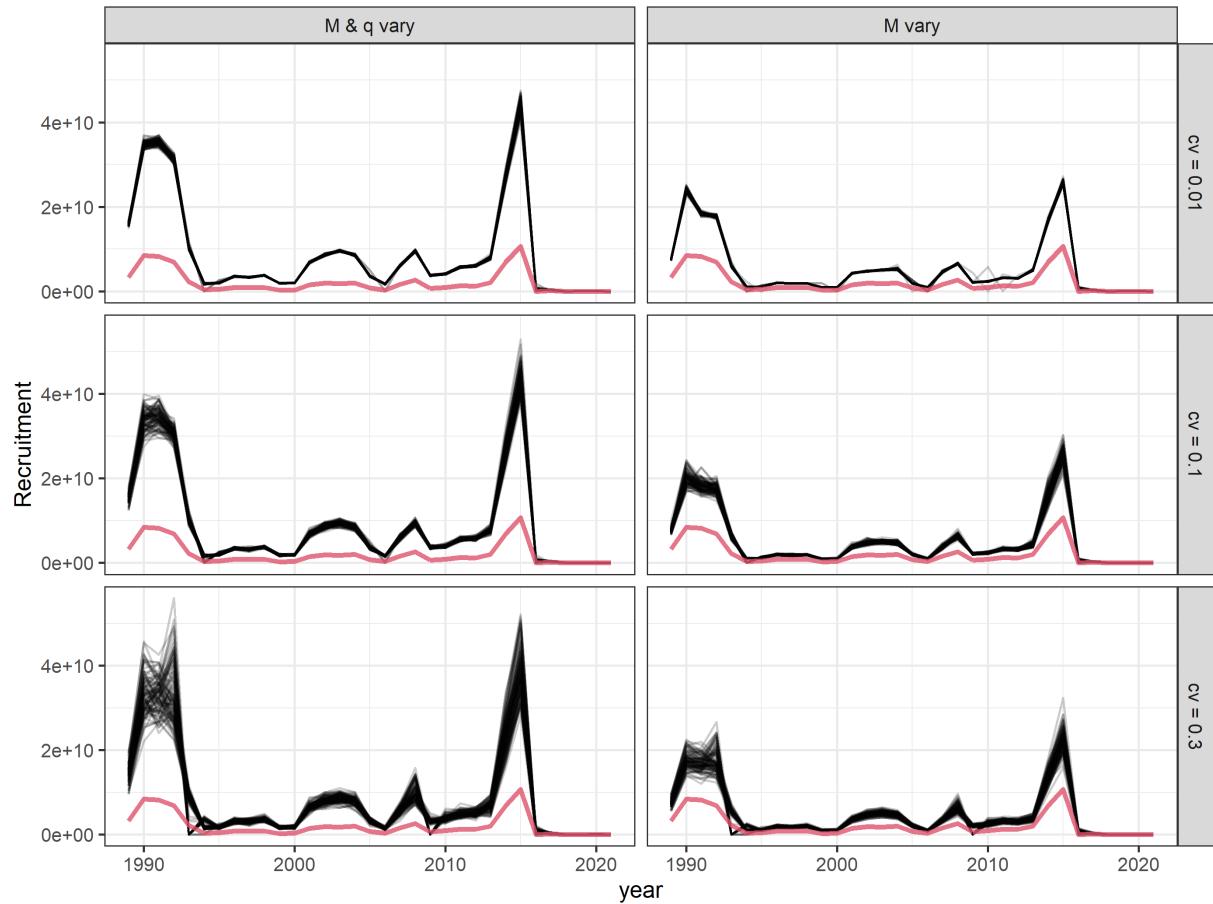


Figure S14: Estimates of recruitment (black lines) compared to the underlying values (red line) from simulations testing the estimation ability of the population dynamics models.

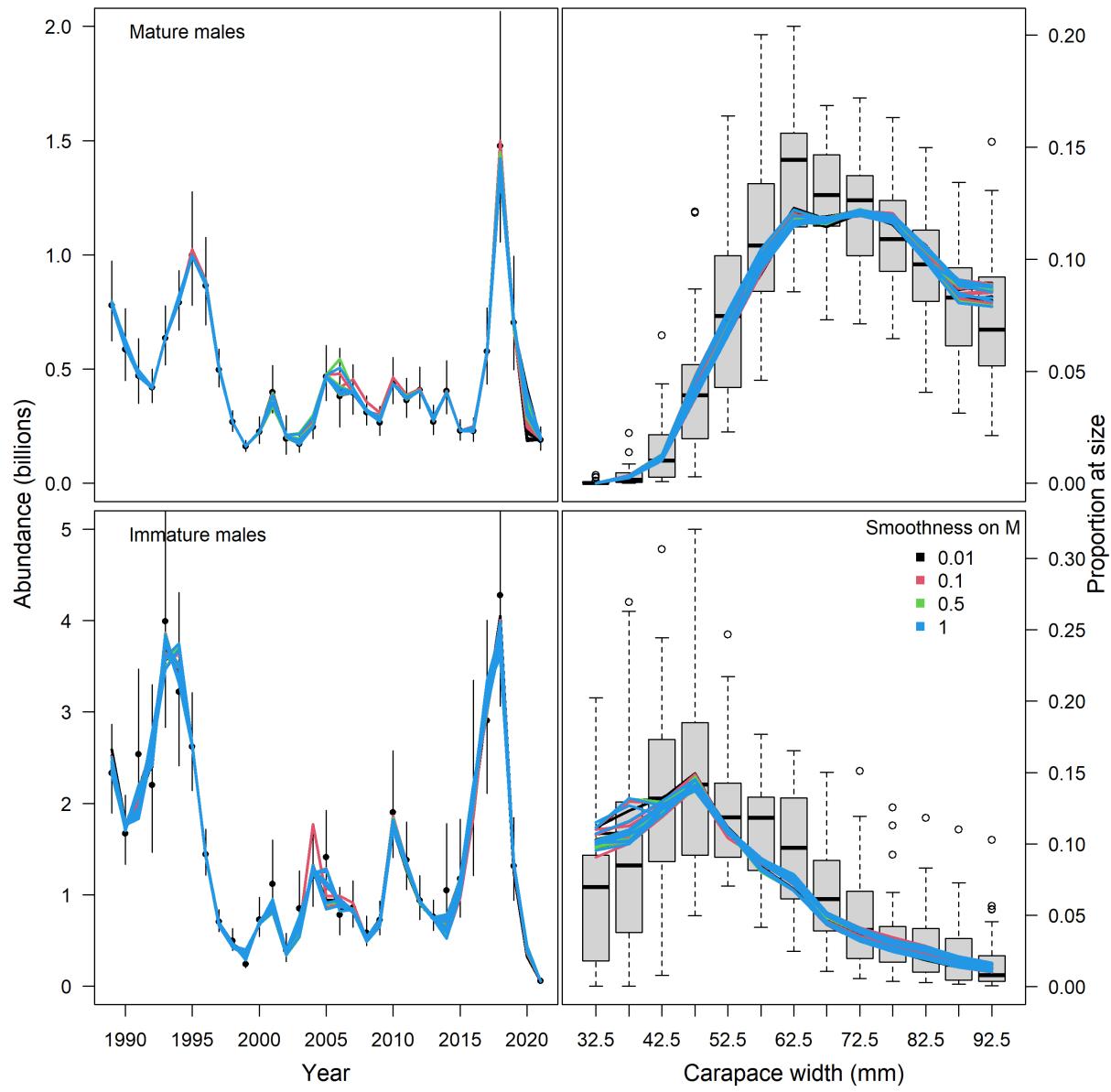


Figure S15: Model fits from sensitivity tests. Indices of abundances are on the left with observations in black dots with 95% confidence intervals; colored lines are model fits. Size composition data are at the right with observations in box plots (aggregated over year; black lines are median, grey box represents 25-75th quantiles, circles are outliers) and colored lines are model fits.

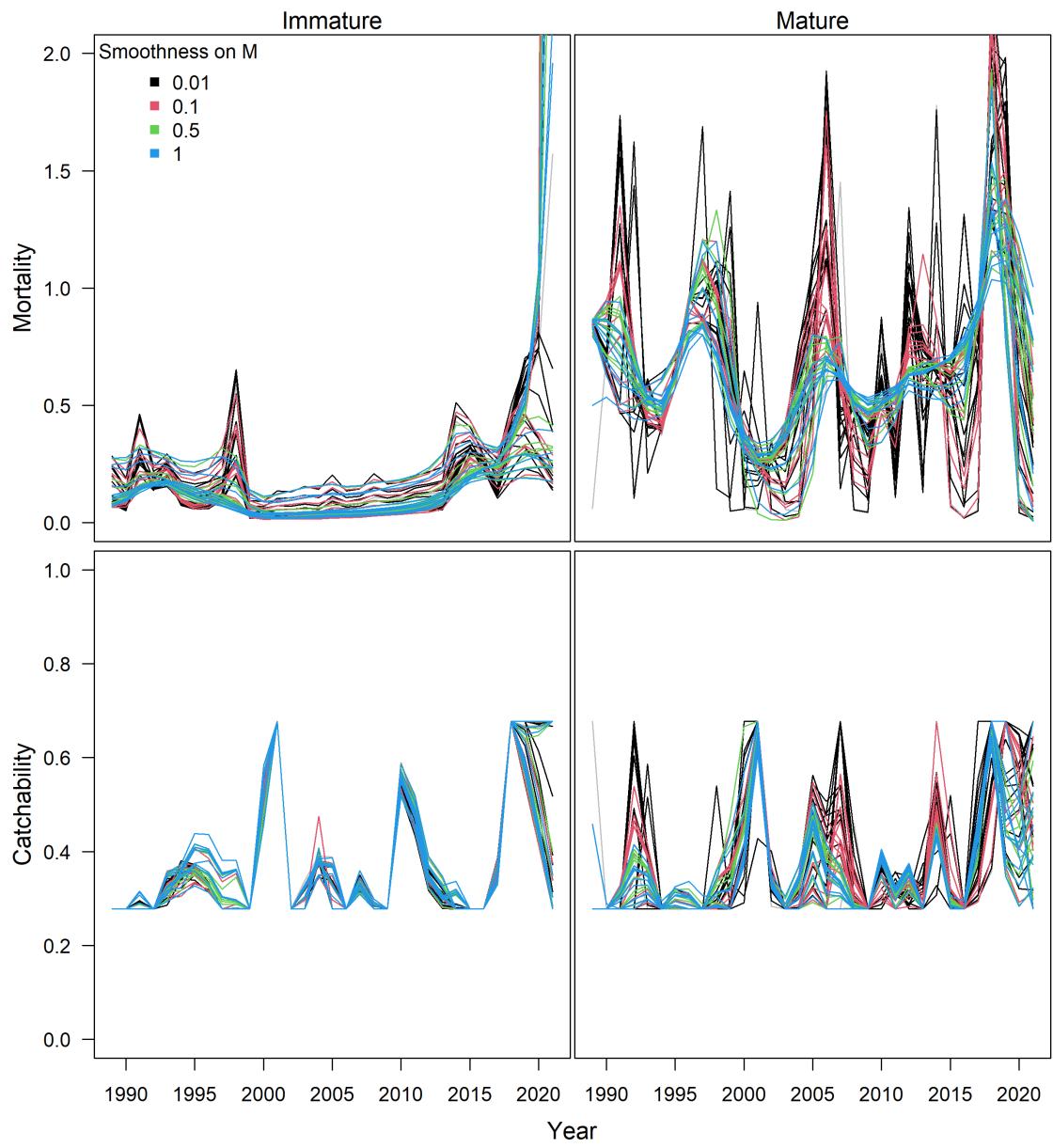


Figure S16: Estimates of mortality and catchability by maturity state over sensitivity runs. Lines are colored based on the smoothness penalty on mortality.

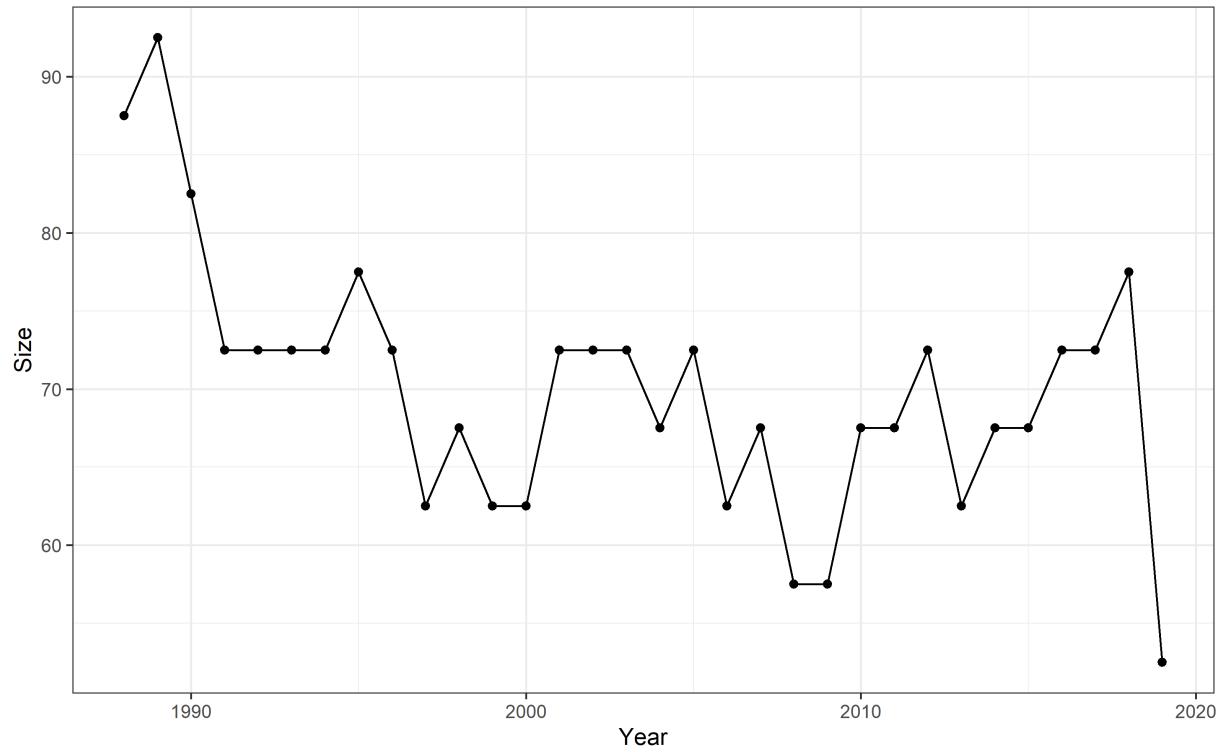


Figure S17: Size (in mm carapace width) at which half of the crab in the population are mature over time (note, this is not the probability of undergoing terminal molt, rather the proportion of the number of mature vs. immature crab at size in the population).

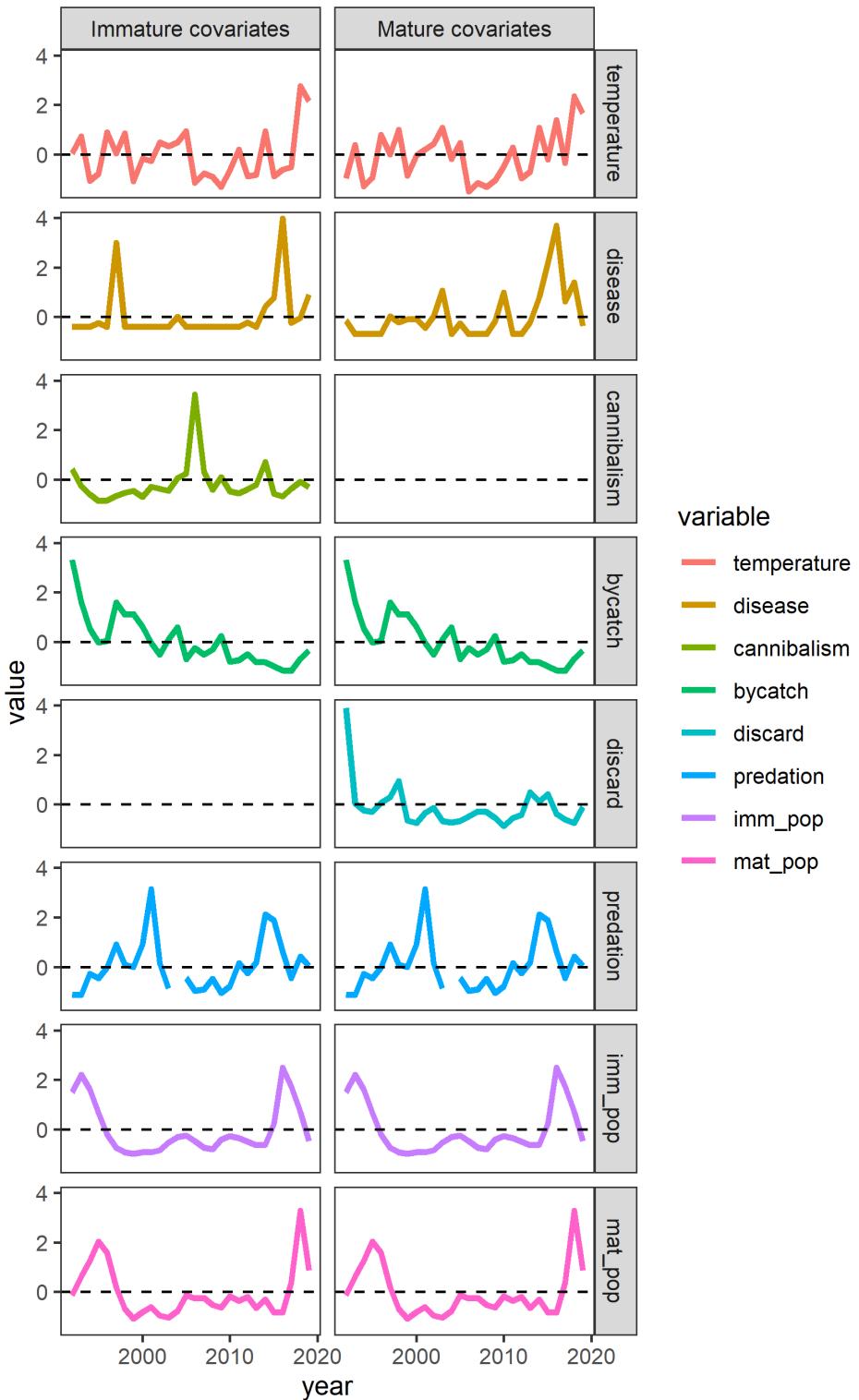


Figure S18: Calculated covariates incorporated into GAMs to relate stressors to estimated mortality. Two covariates (discard and predation) are only relevant for one maturity state based on the critical role size plays in the process (i.e. discards are primarily relatively large crab and predation is primarily smaller crab).

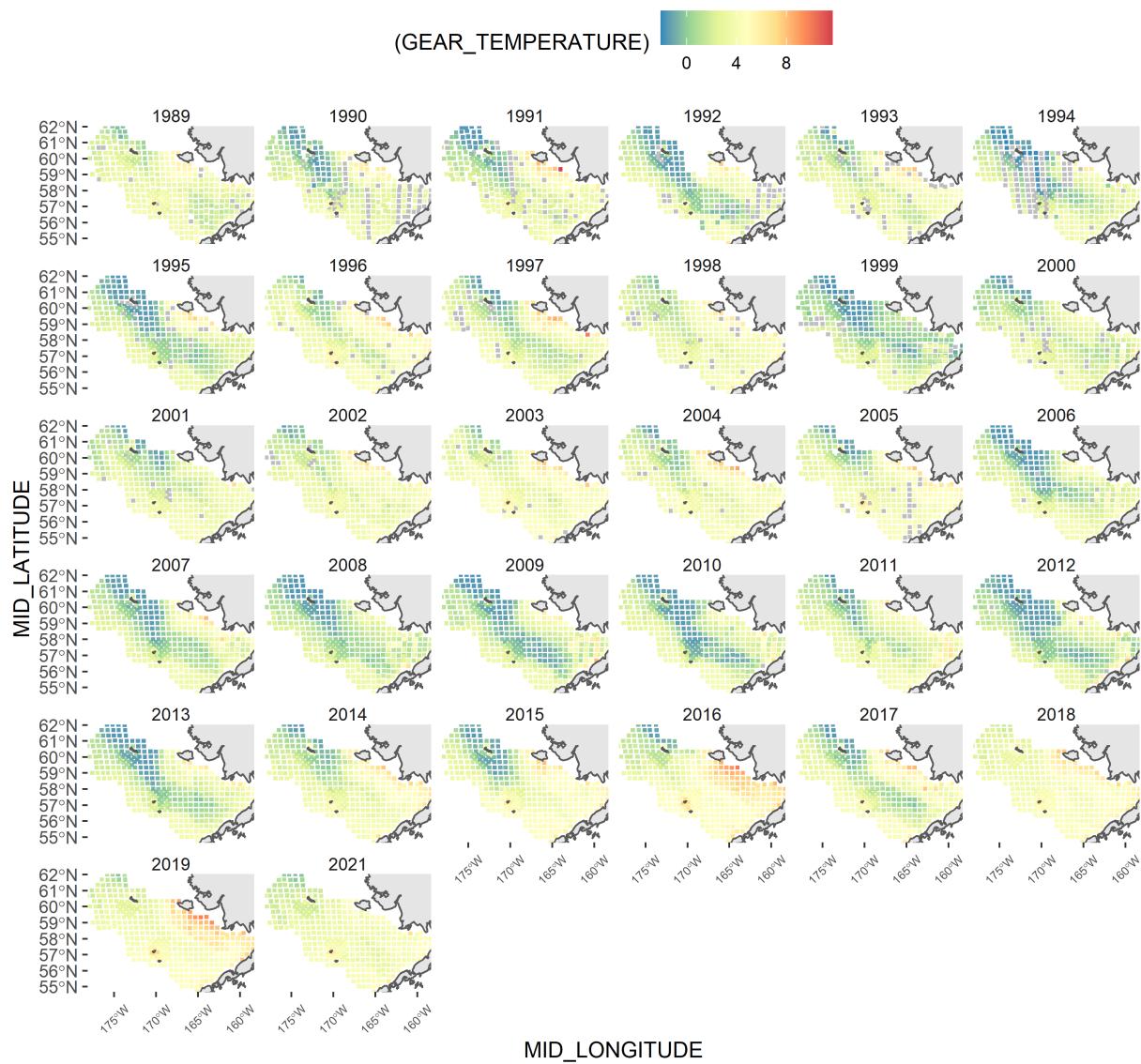


Figure S19: Observed bottom temperature at the time of the NMFS summer survey. Less than 2 degrees C represents the cold pool, seen in green and blue here.

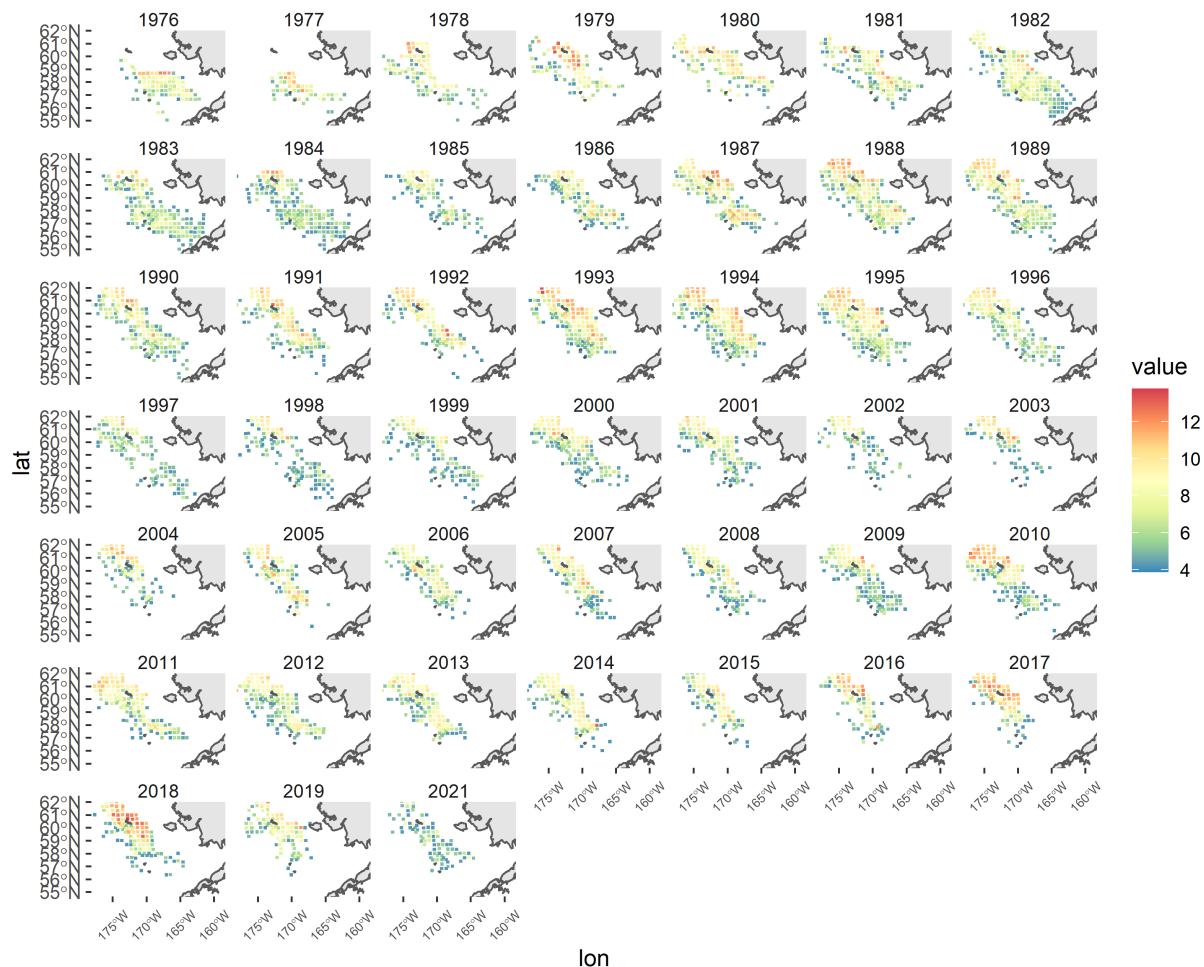


Figure S20: Distribution and intensity of densities (in log numbers) of crab <55 mm carapace width in the NMFS summer survey.

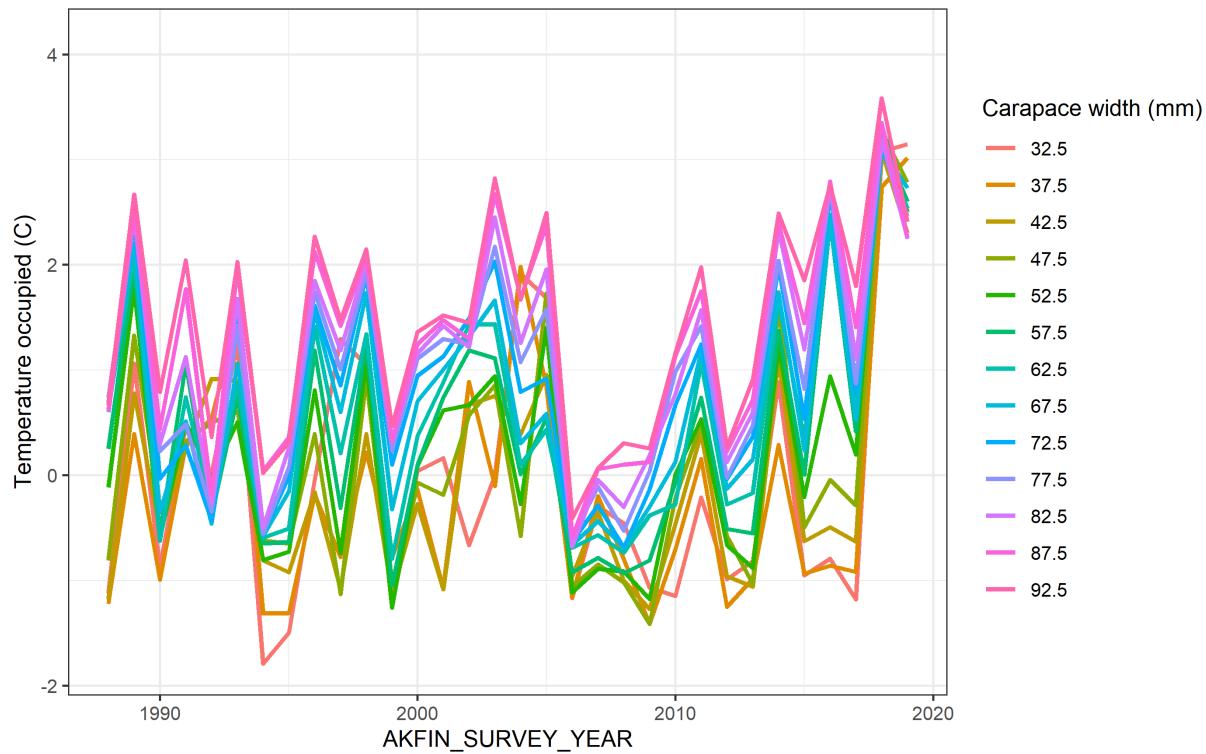


Figure S21: Average temperature occupied over time of crab by 5 mm size bin.

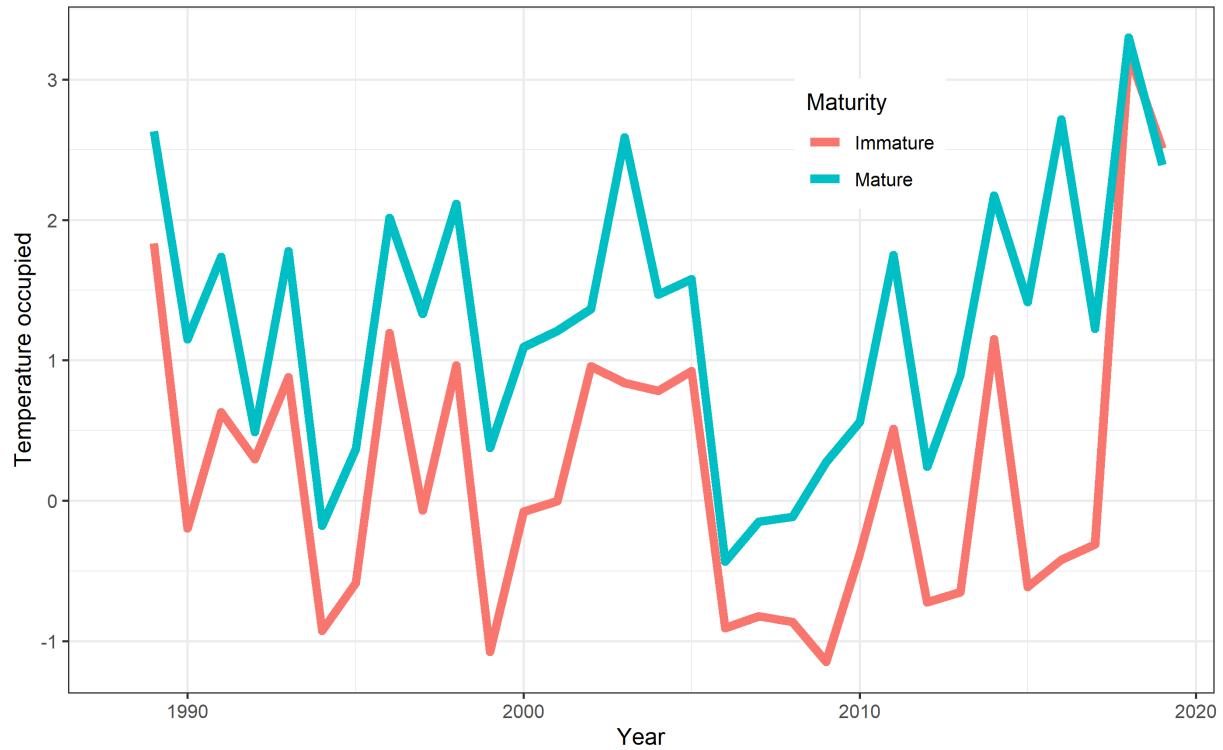


Figure S22: Average temperature occupied over time of crab by maturity state defined by the size at which 50% of crab are mature according to chela height.

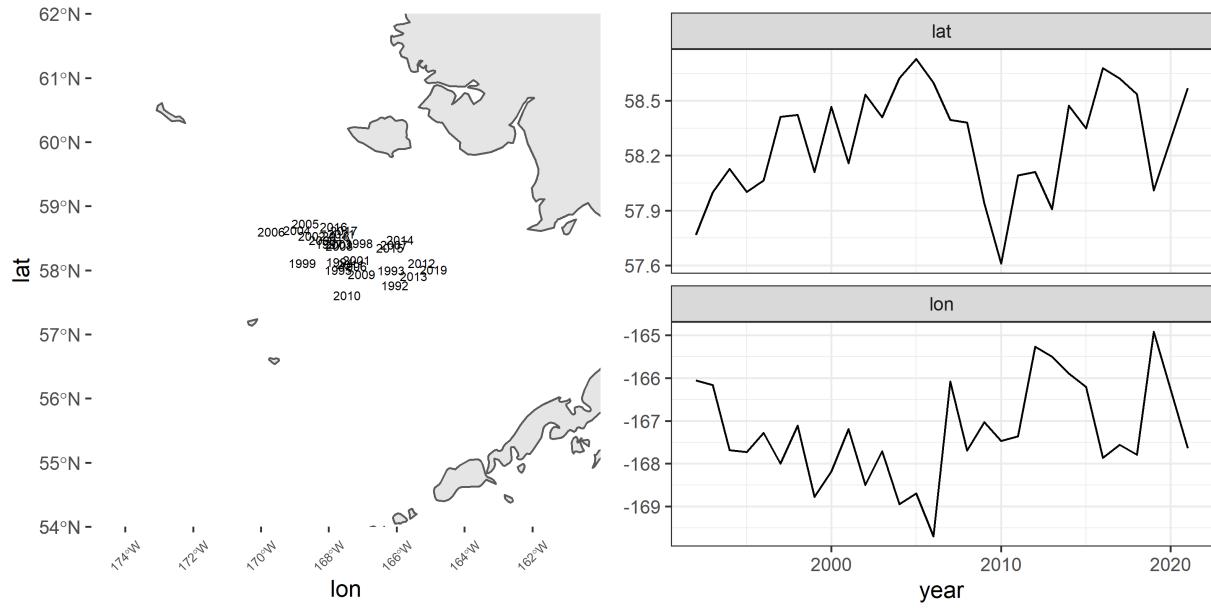


Figure S23: Centroids of abundance for Pacific cod in the Bering Sea over time (left). Right panels show the time series of the centroids broken down by latitudinal and longitudinal components.

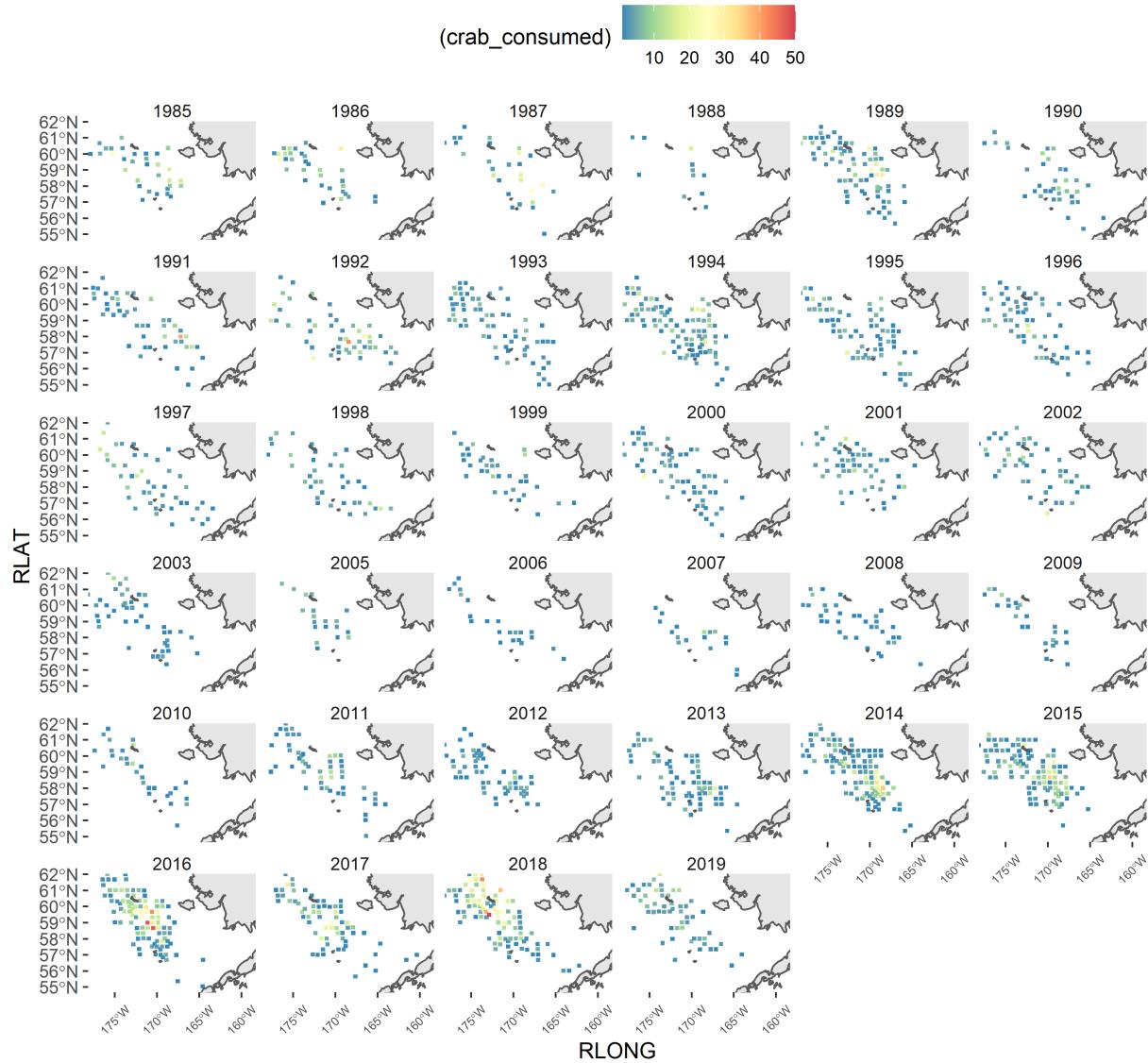


Figure S24: Location and number of crab observed in cod stomachs over time. These are the raw data used to calculate crab consumption by cod and have not been adjusted for sampling effort, but provide background for the spatial distribution of predation over time.

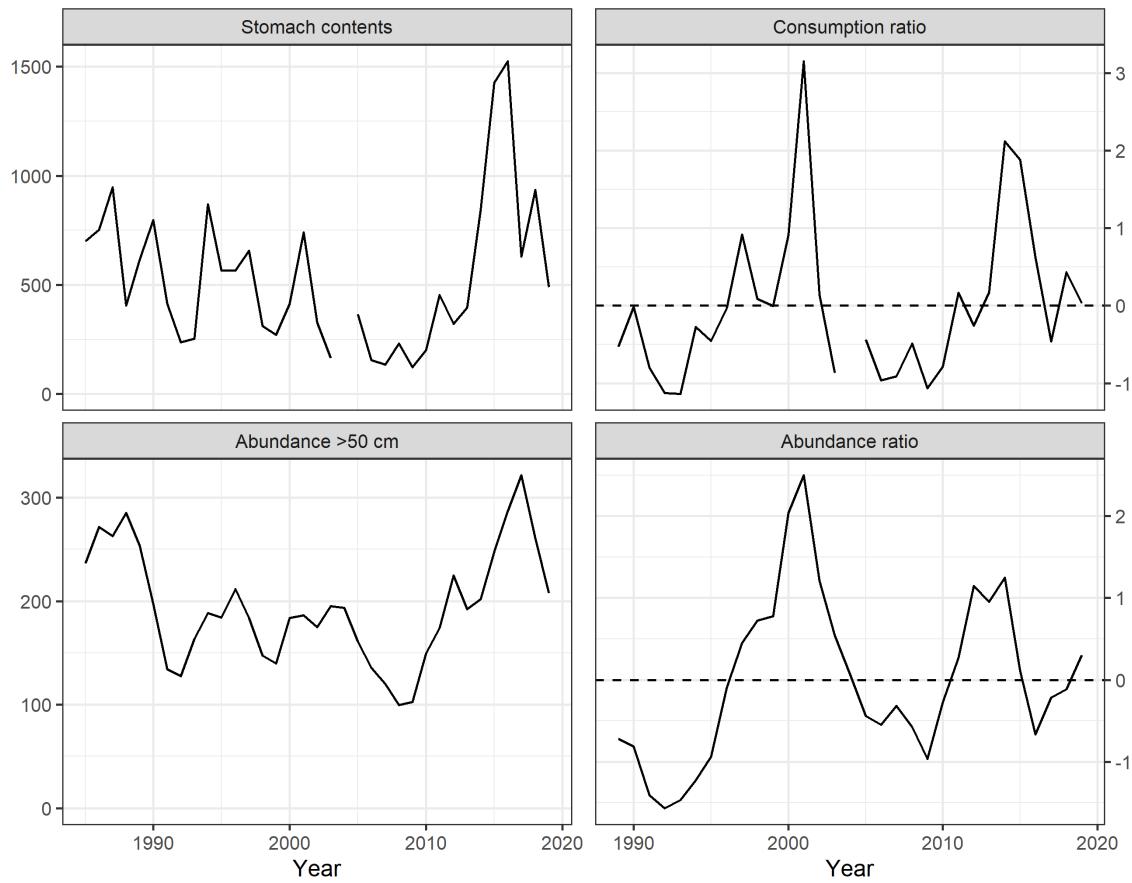


Figure S25: A comparison of indices of cod predation on snow crab. Left column are the calculated consumption of crab by cod (top) and the raw numbers of cod greater than 50 cm. The right column is the left column divided by the estimated number of crab in the eastern Bering Sea.

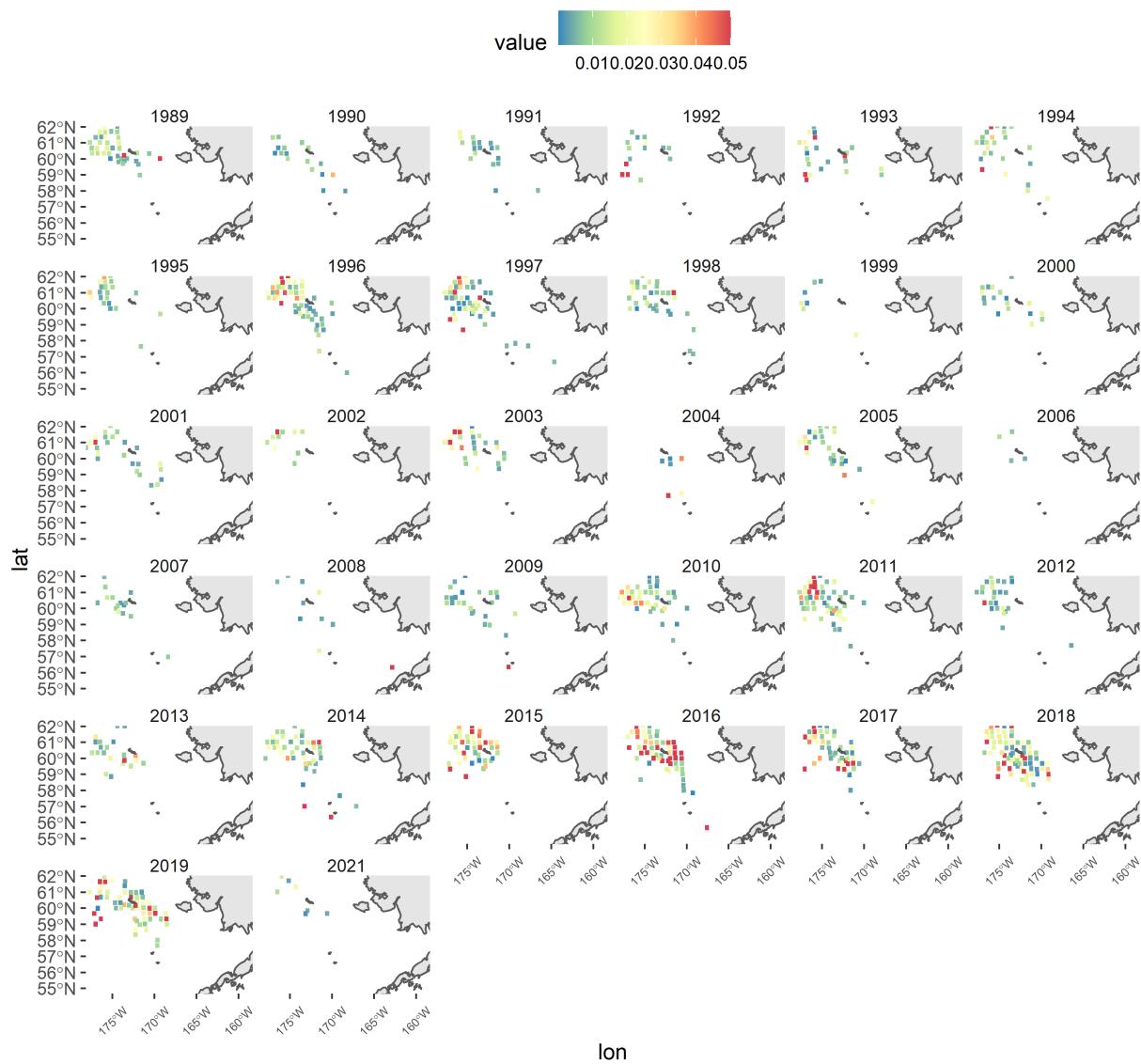


Figure S26: Location and intensity of bitter crab disease over time from visual prevalence observations in the NMFS summer survey.

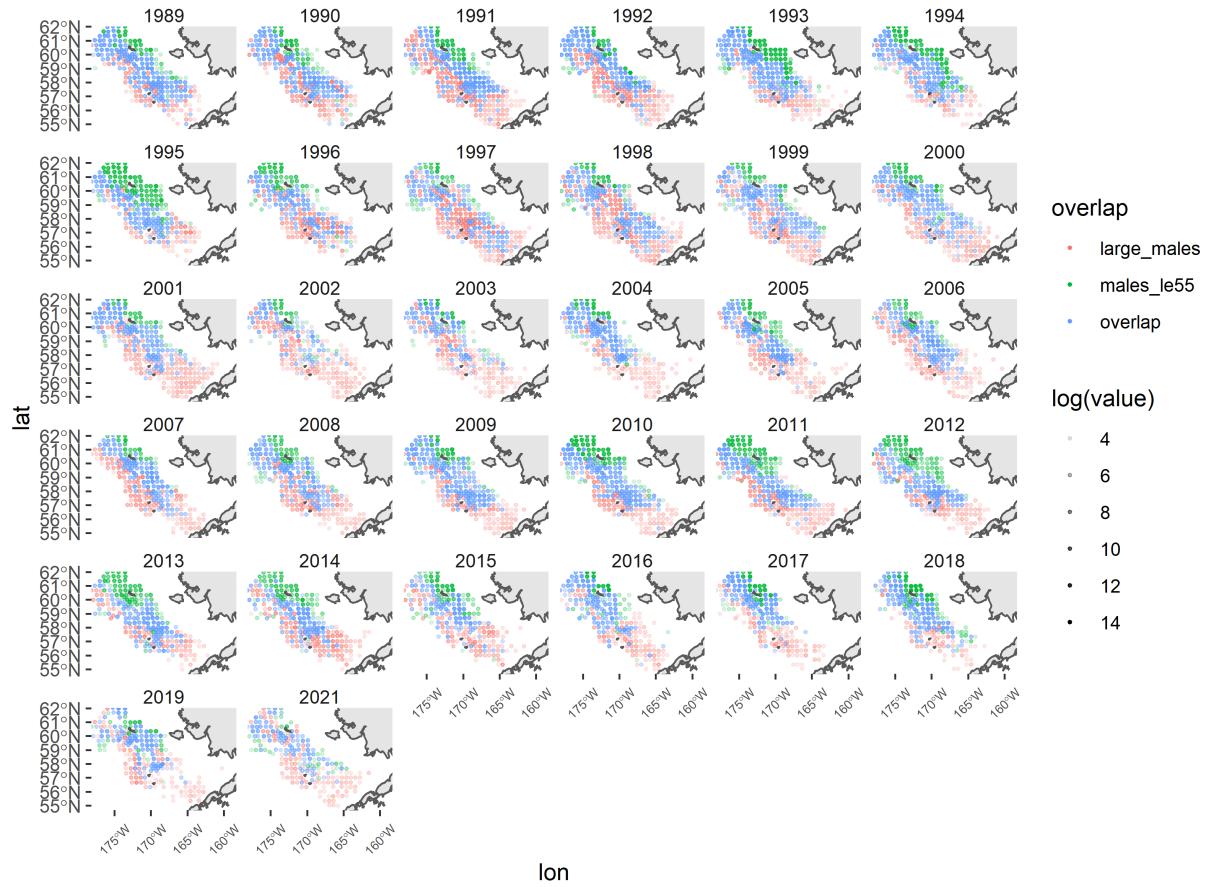


Figure S27: Overlap of large males ( $>95$  mm carapace width) and males smaller than 55 mm carapace width. Opacity of the dot represents the density of crab. Blue represents overlapping distribution. Green and red represent non-overlapping observations of small and large males, respectively.

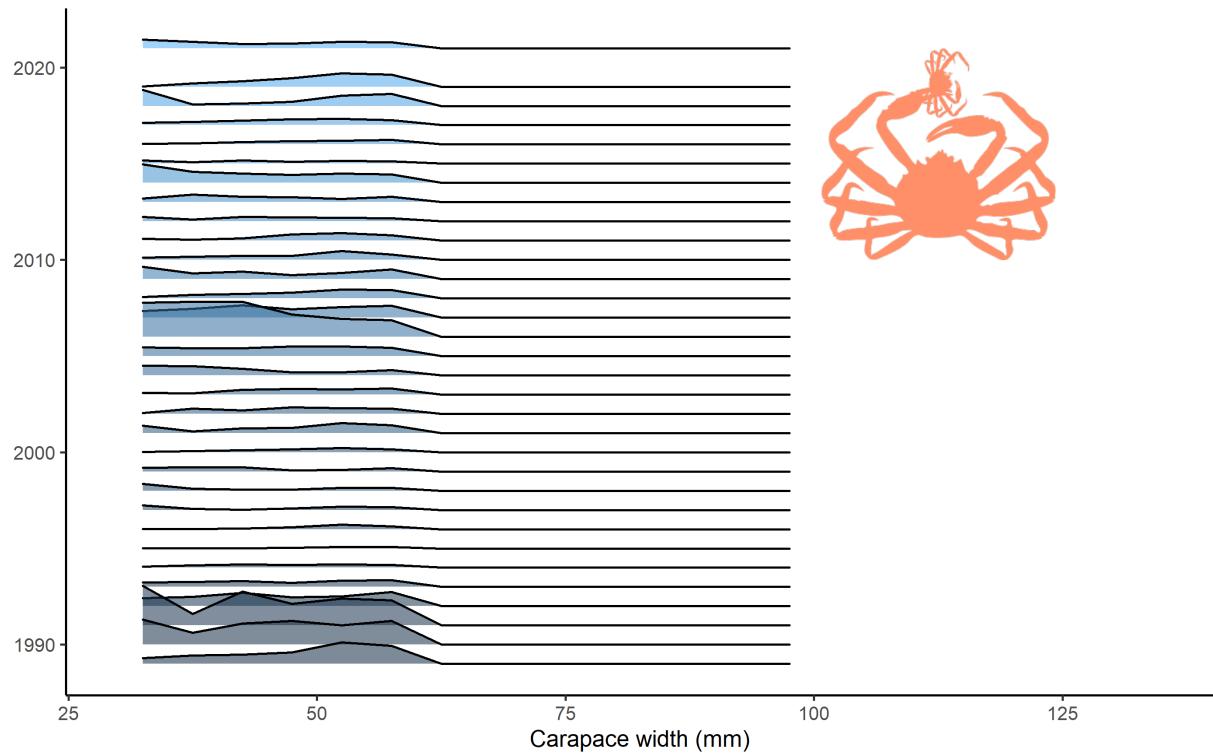


Figure S28: Relative risk at size for cannibalism over time.

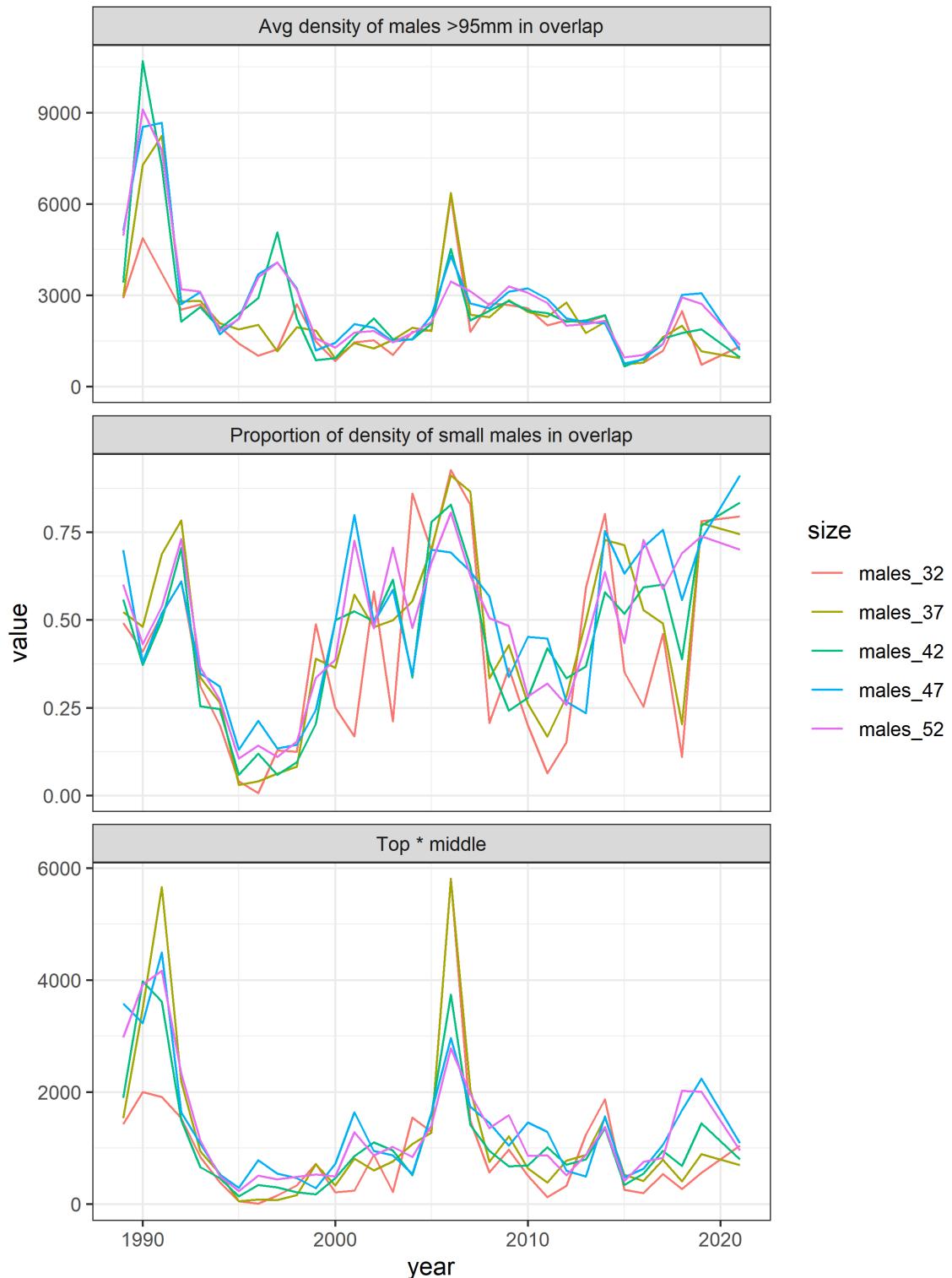


Figure S29: Times series by size of the density of large males in overlapping space (top), the proportion of small males in the overlapping area (middle), and the product of the two (bottom), which is used as an index of cannibalism in the models relating estimated mortality to environmental stressors.

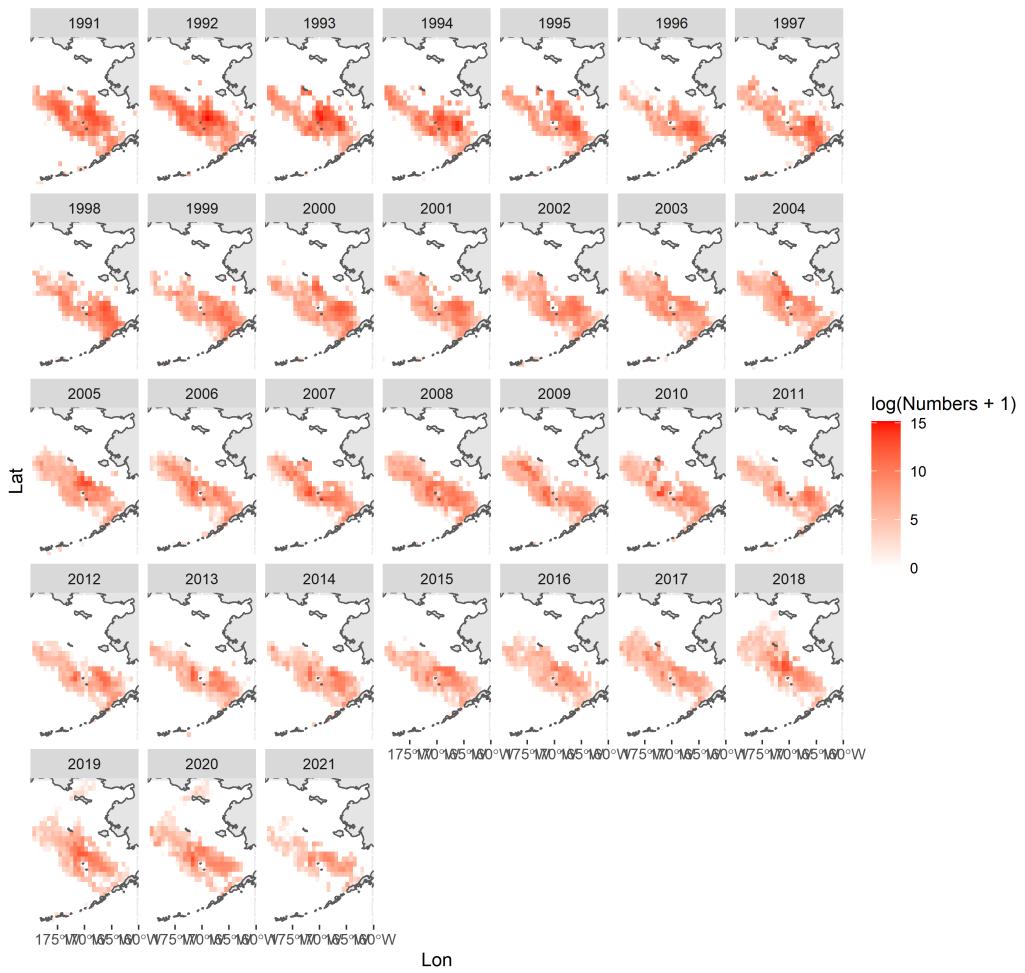


Figure S30: Location and intensity of bycatch of snow crab over time in log space.

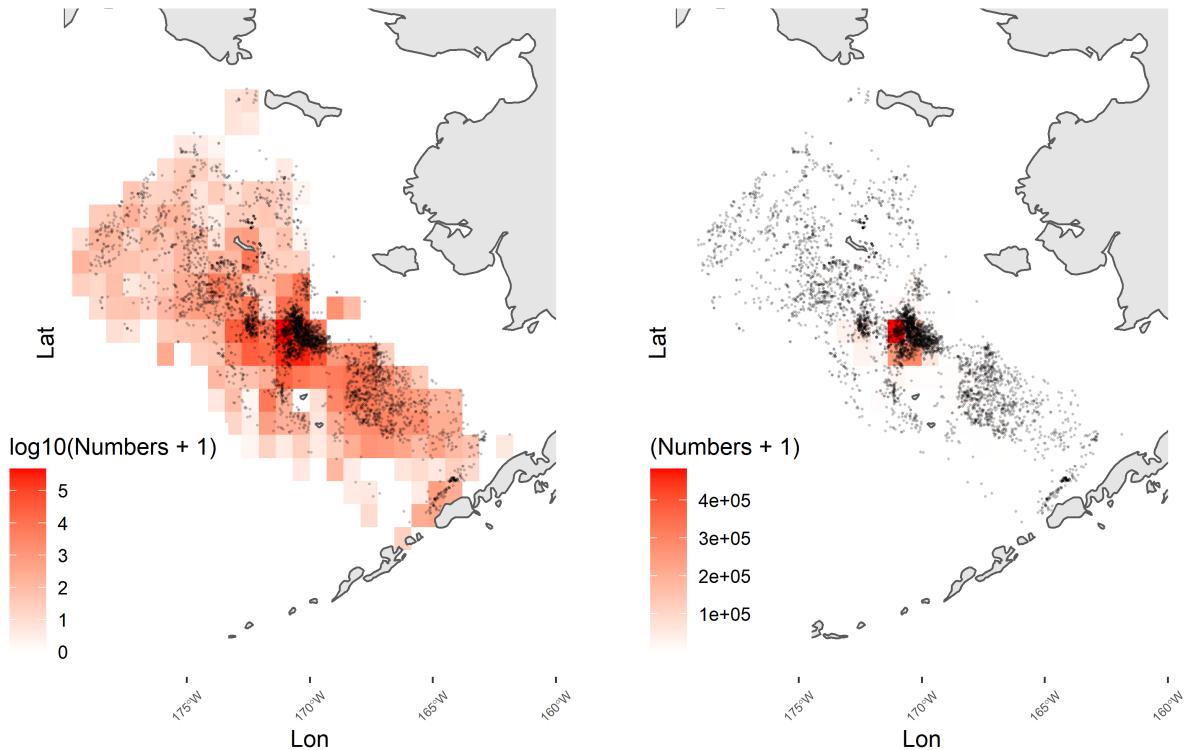


Figure S31: Comparison of location and intensity of bycatch in 2018 for natural and log space.

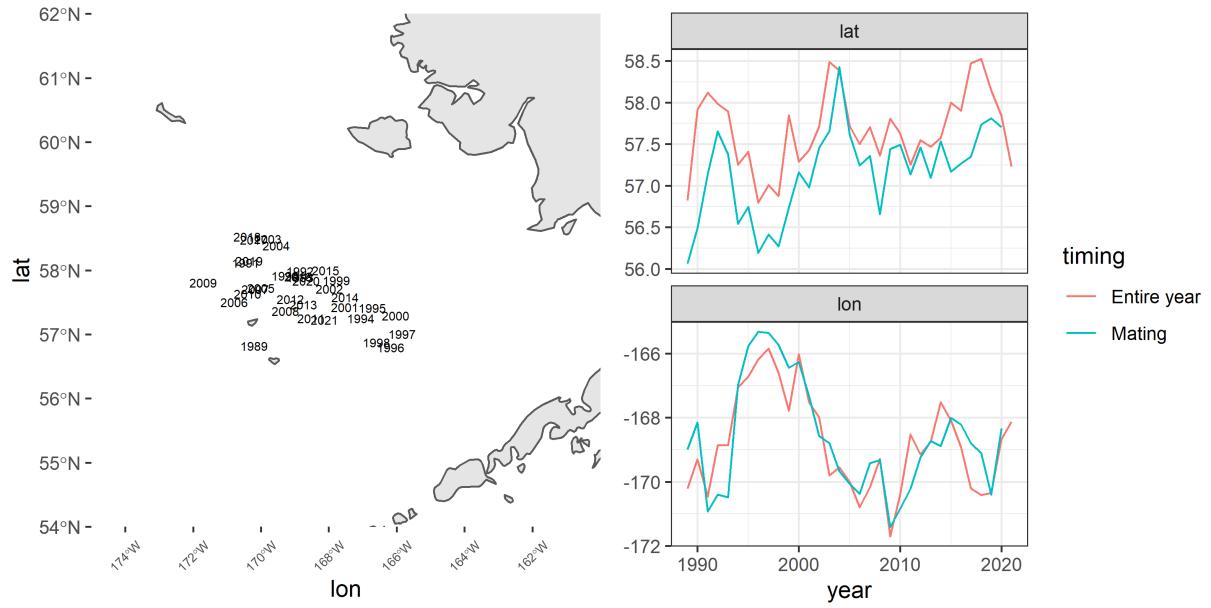


Figure S32: Centroids of bycatch over time calculated over the entire year (left). Centroids broken into time series of latitudinal and longitudinal components calculated over the entire year and during the months December through March which roughly overlap with mating.

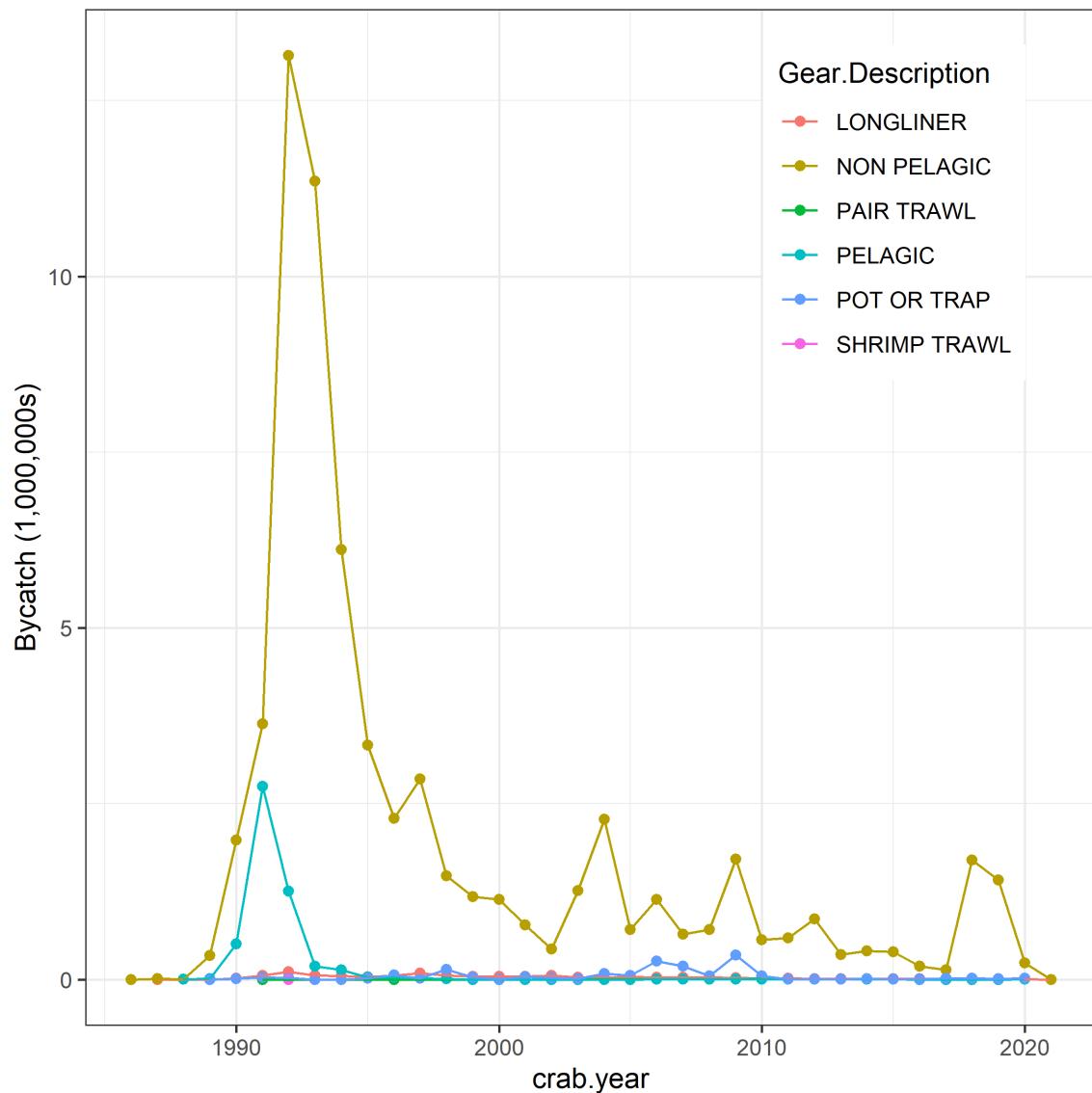


Figure S33: Bycatch in numbers by gear types reported from NMFS observer programs.

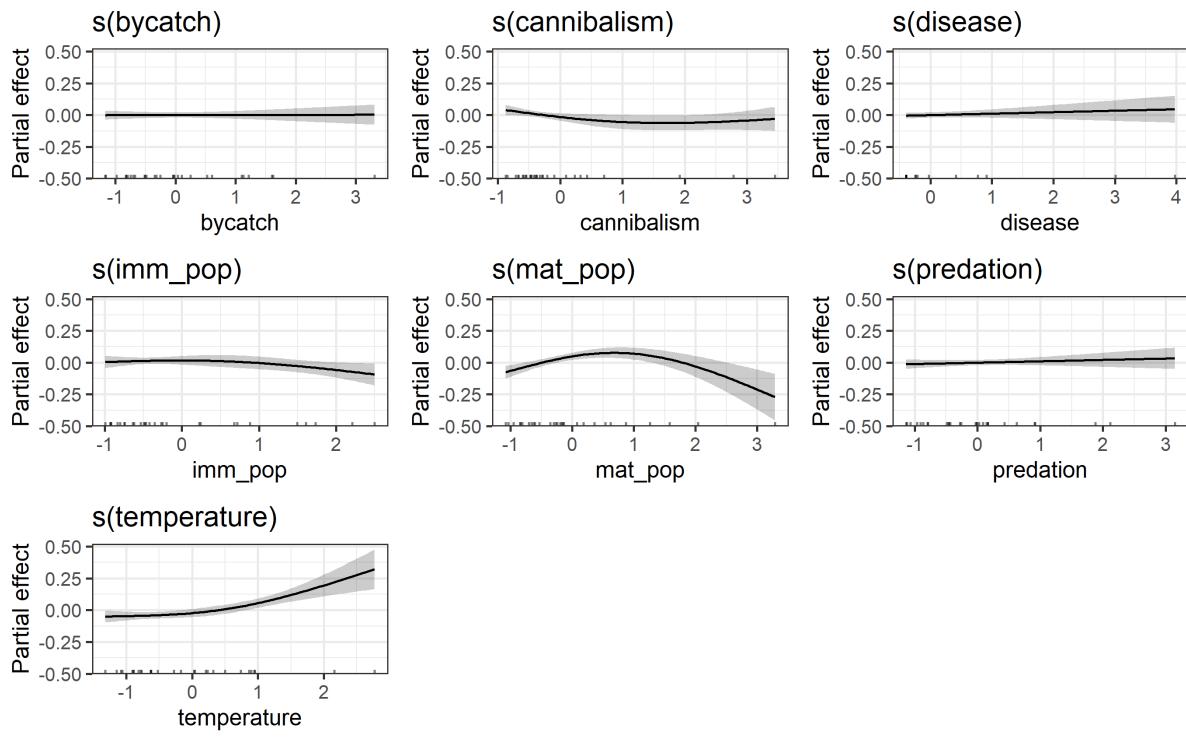


Figure S34: Smooths resulting from the full model estimating the relationship between environmental covariates and immature mortality.

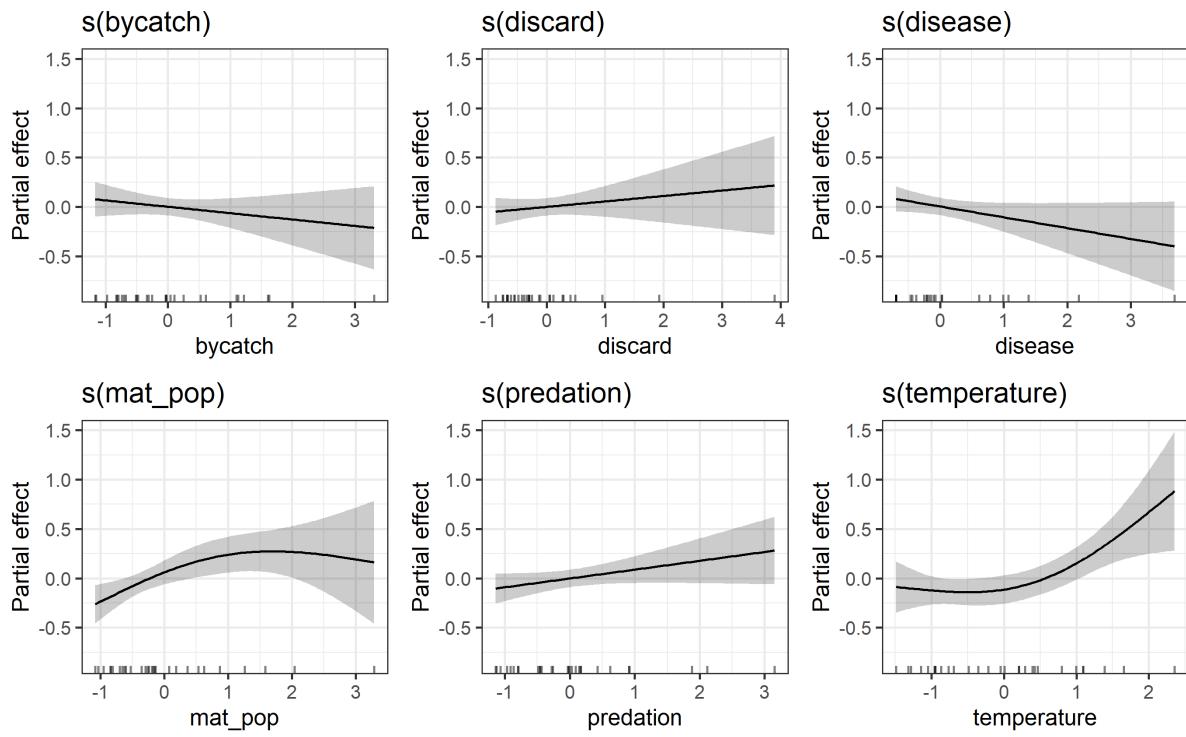


Figure S35: Smooths resulting from the full model estimating the relationship between environmental covariates and mature mortality.

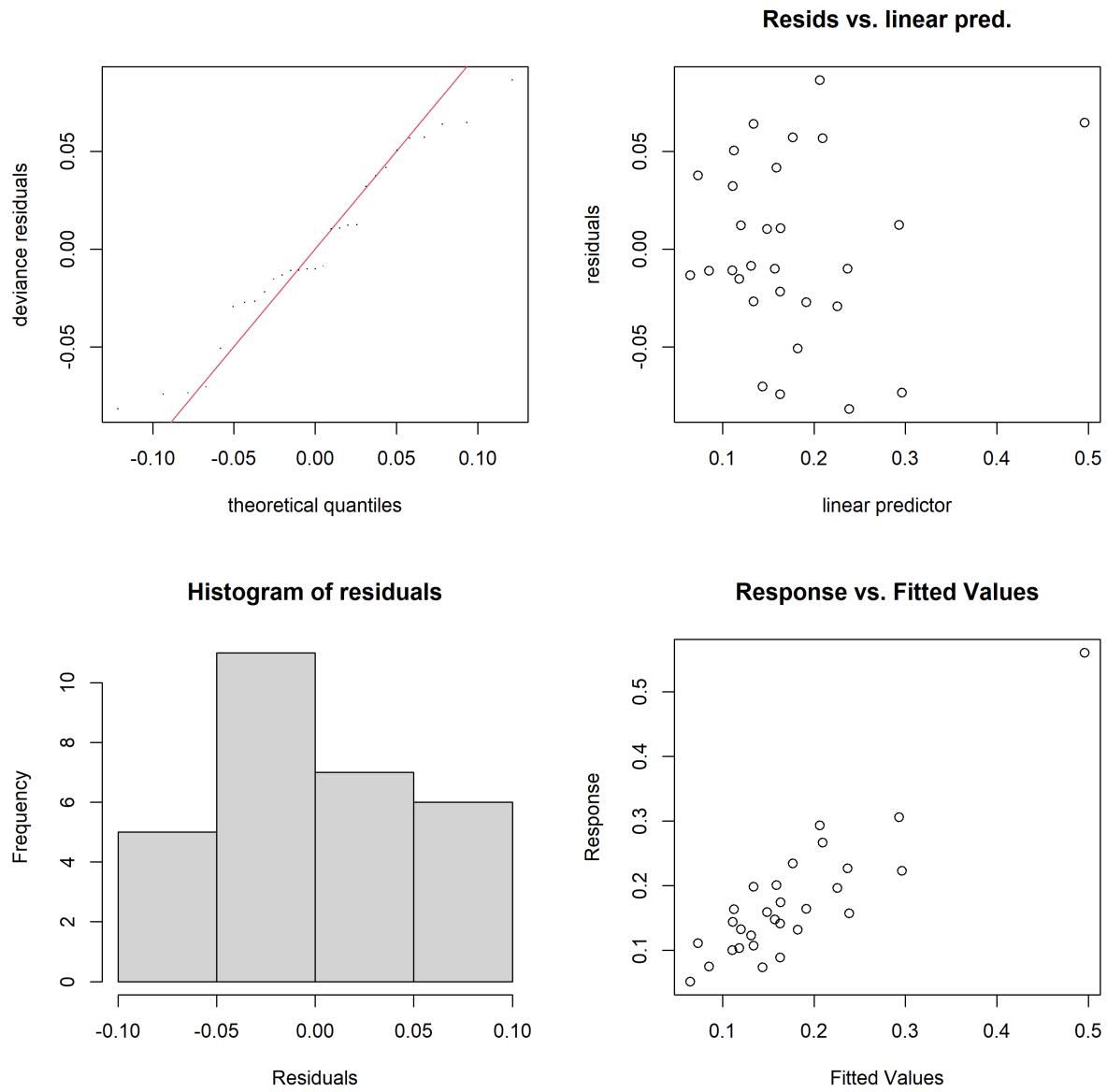


Figure S36: Diagnostic plots for the full model relating immature mortality and environmental stressors.

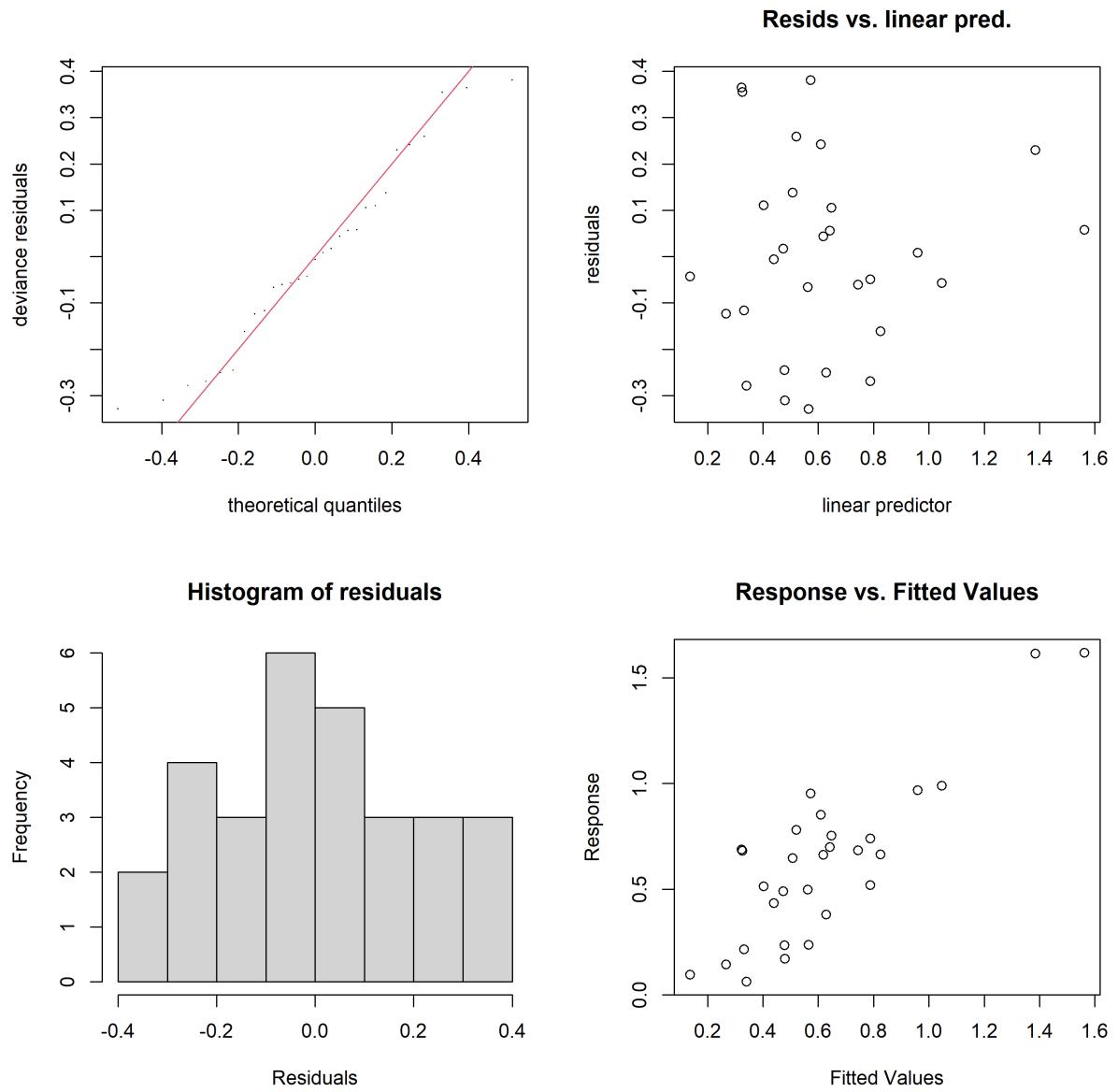


Figure S37: Diagnostic plots for the full model relating mature mortality and environmental stressors

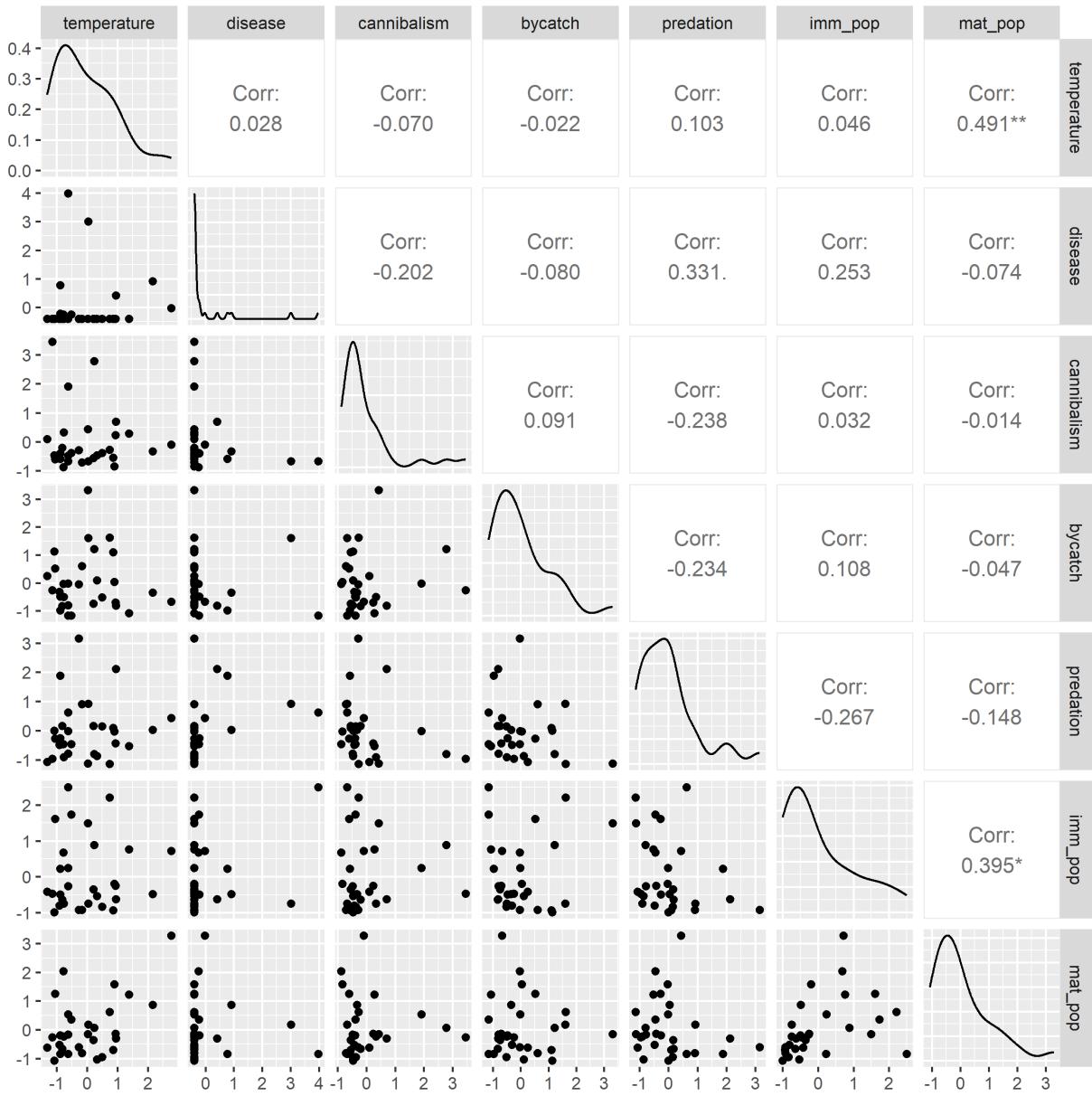


Figure S38: Pairs plots displaying the correlation between covariates for immature crab. Diagonal represents the distribution of a given variable.

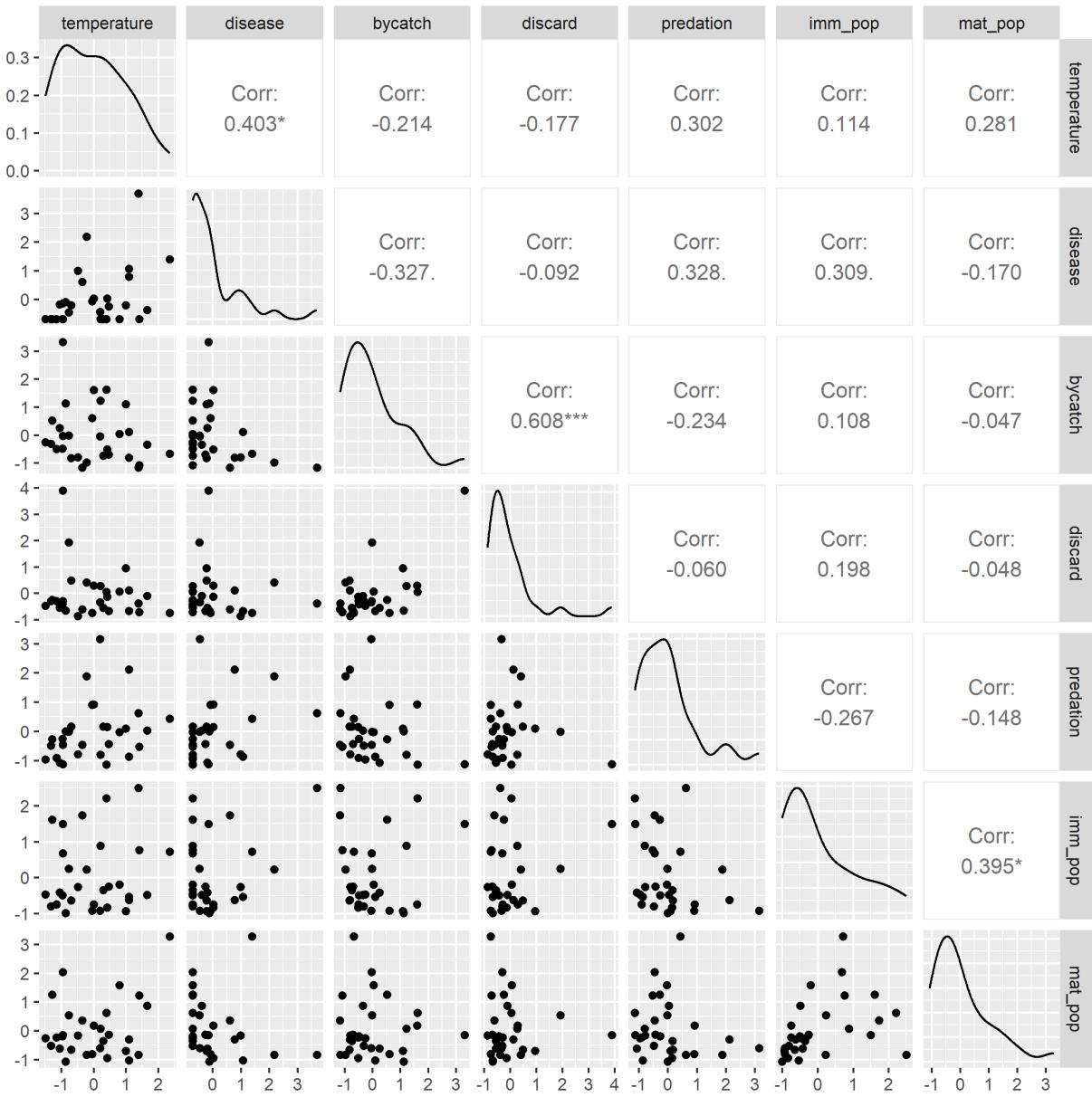


Figure S39: Pairs plots displaying the correlation between covariates for mature crab. Diagonal represents the distribution of a given variable.

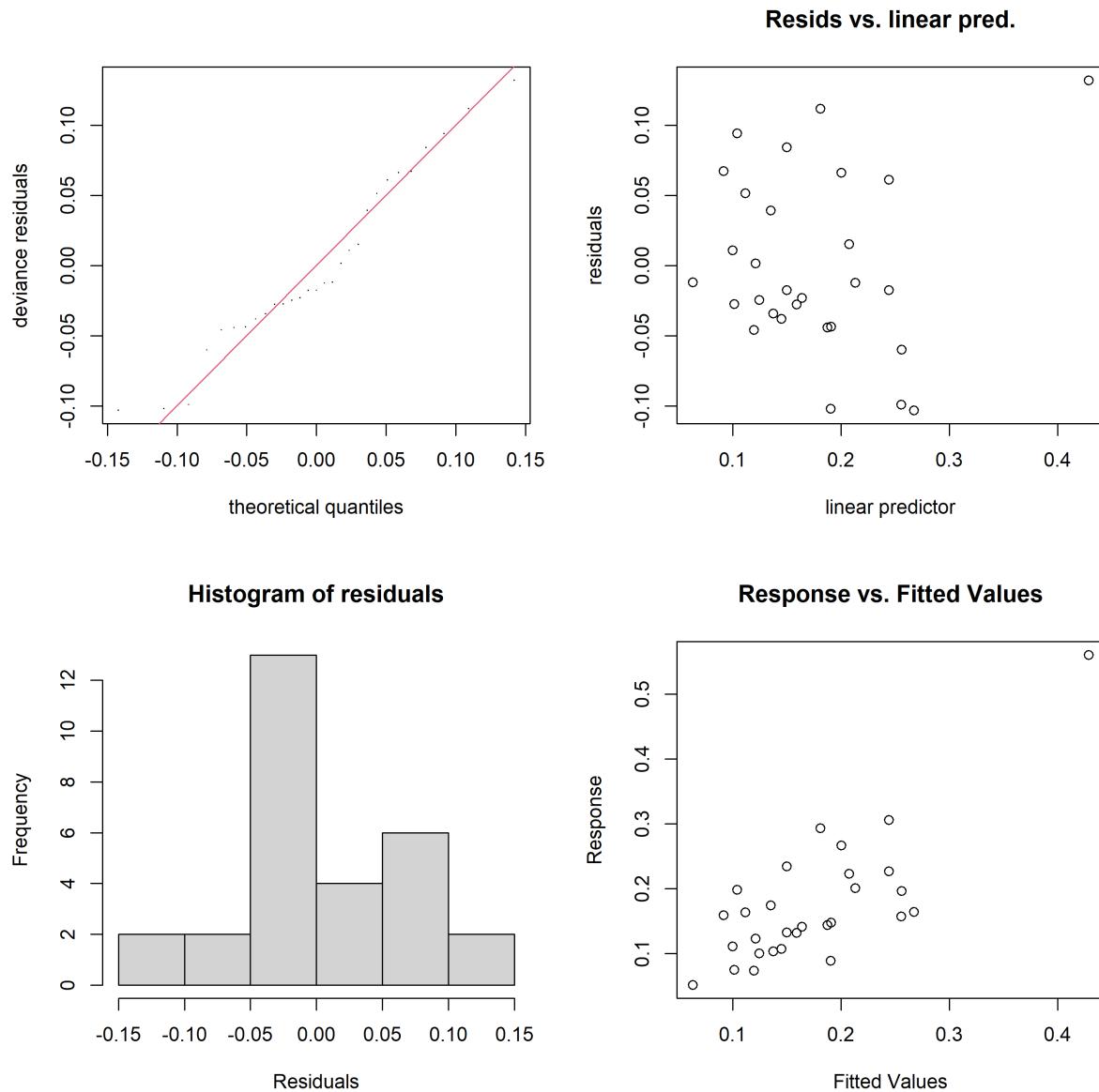


Figure S40: Diagnostic plots for the trimmed model relating immature mortality and environmental stressors.

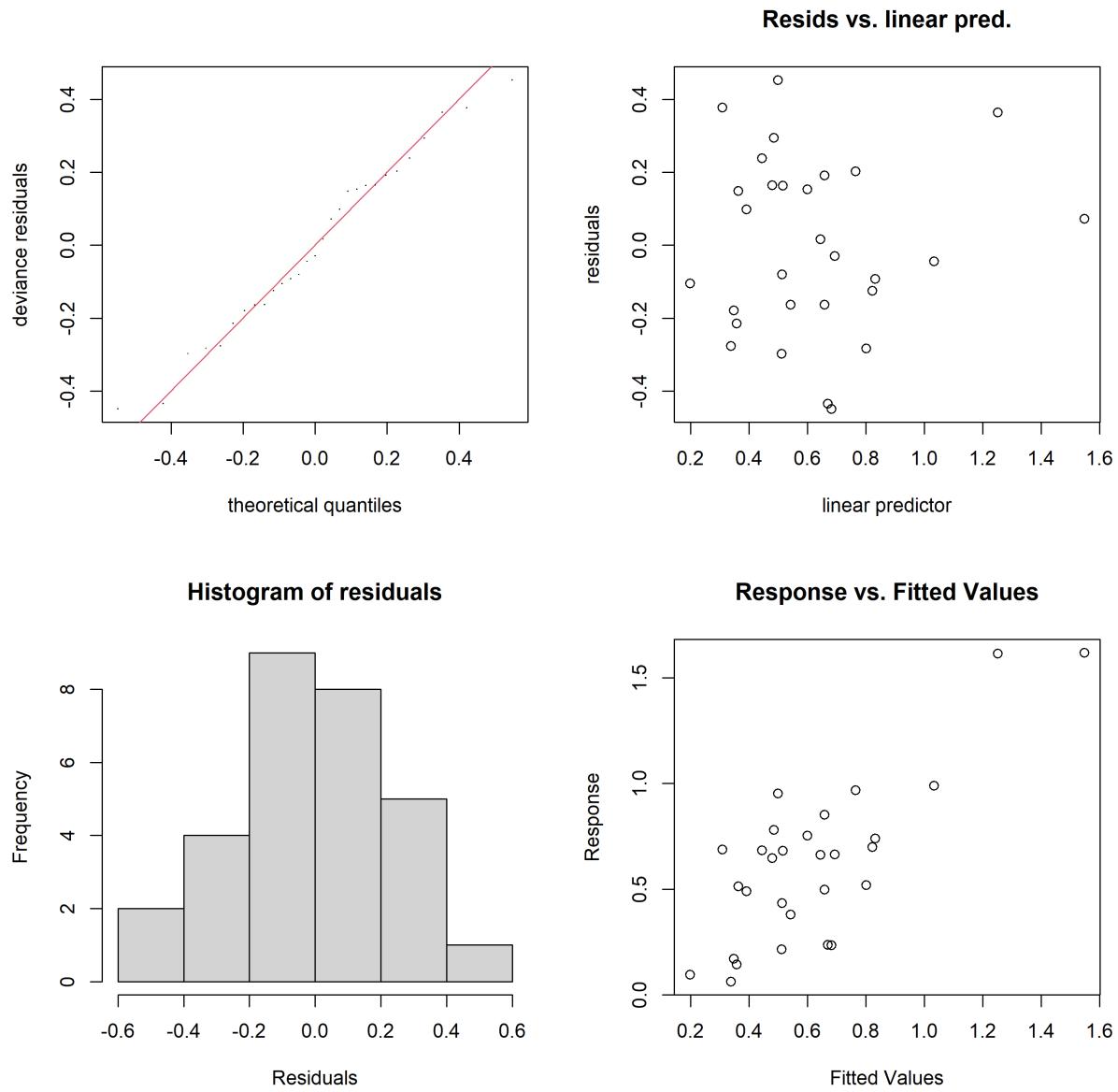


Figure S41: Diagnostic plots for the trimmed model relating mature mortality and environmental stressors.

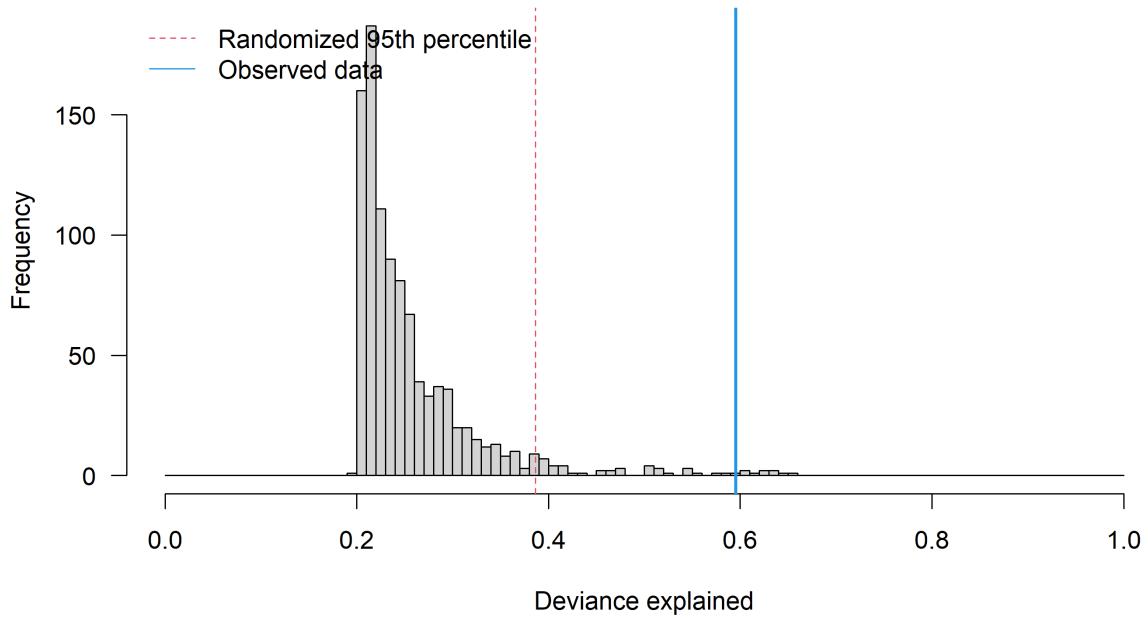


Figure S42: Results of randomization trials for the trimmed model relating estimated immature mortality to environmental stressors. Grey bars represent the number of trials in which the randomized model explained the deviance on the x-axis. Dashed vertical red line represents the 95th quantile of the deviance explained by the randomized trials. Blue line represents the deviance explained with the real data.

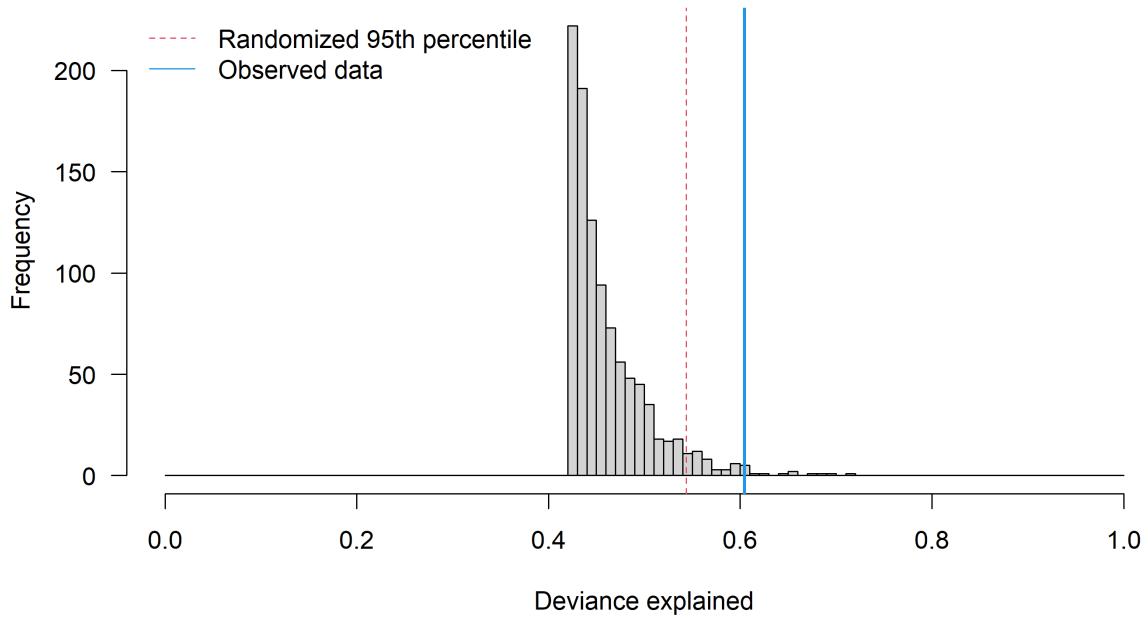


Figure S43: Results of randomization trials for the trimmed models relating estimated immature mortality to environmental stressors. Grey bars represent the number of trials in which the randomized model explained the deviance on the x-axis. Dashed vertical red line represents the 95th quantile of the deviance explained by the randomized trials. Blue line represents the deviance explained with the real data.

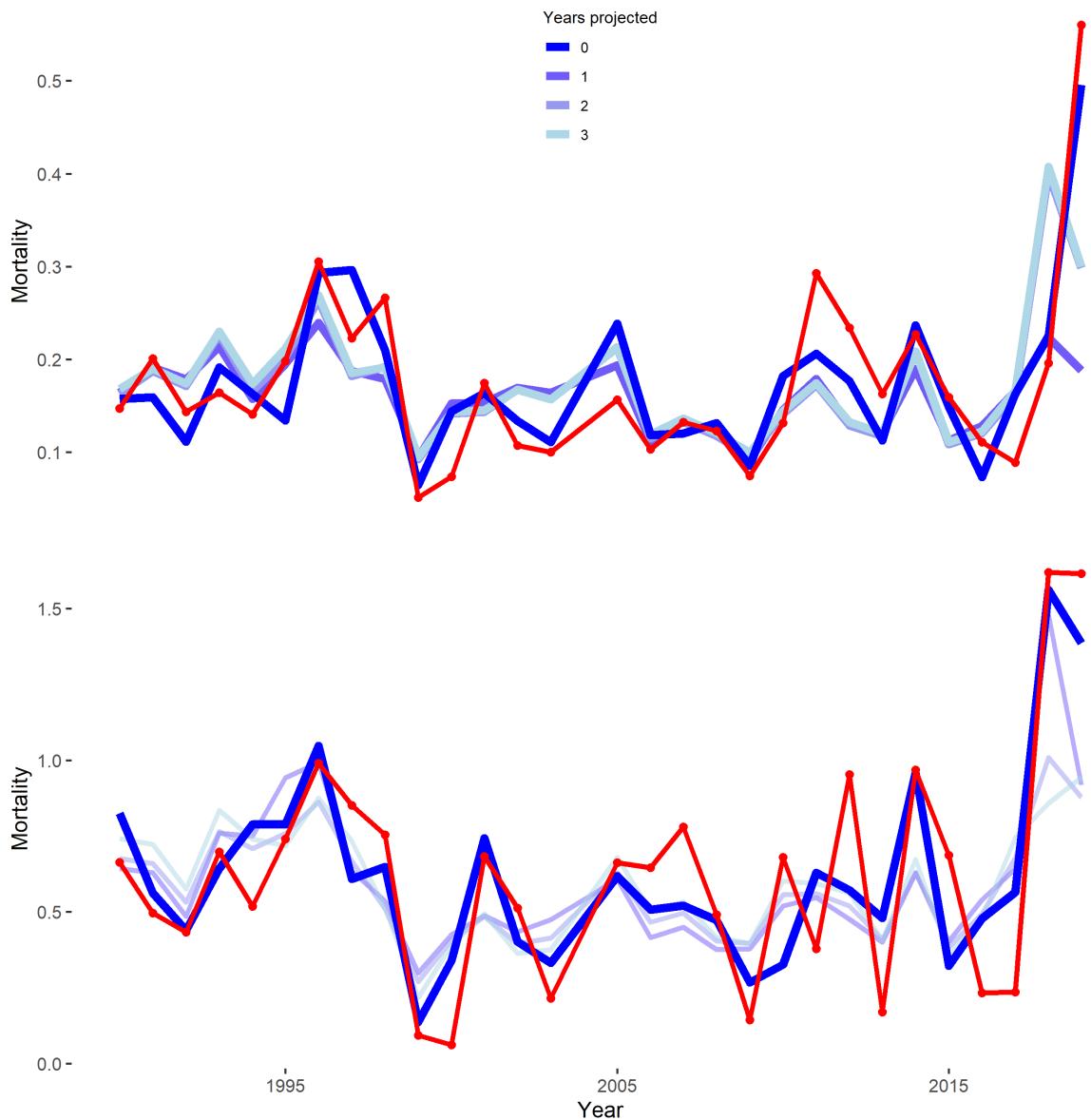


Figure S44: Predictive skill of the GAMs for immature and mature mortality. Reproduced from figure 2 in the main text to provide better detail.

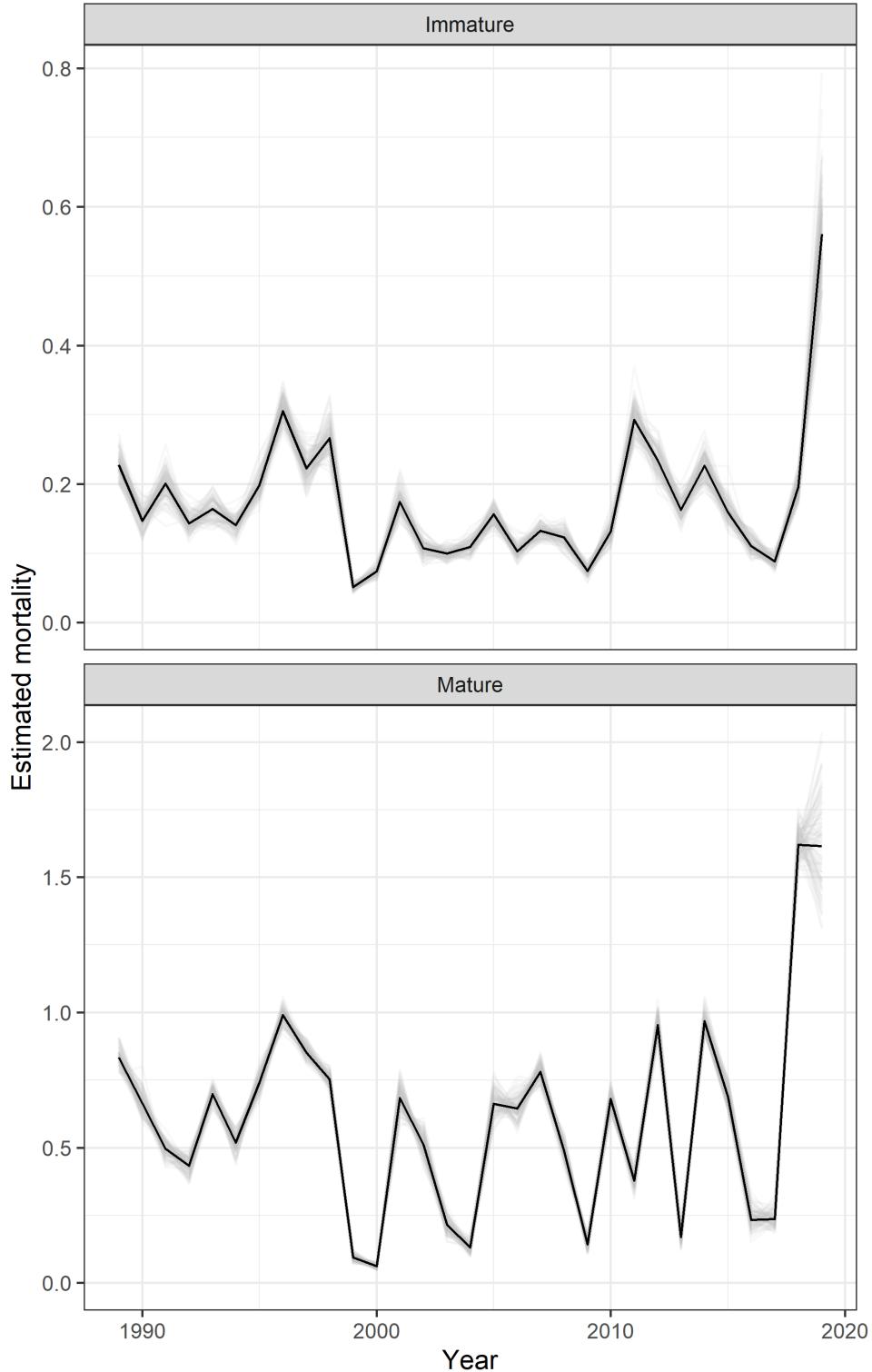


Figure S45: Simulated time series of estimated immature and mature mortality that incorporate the uncertainty associated with the fitting process of the population dynamics model. Each grey line represents one iteration of multiplying the maximum likelihood estimates of the mortality deviations by the covariance matrix. The black line represents the MLE.

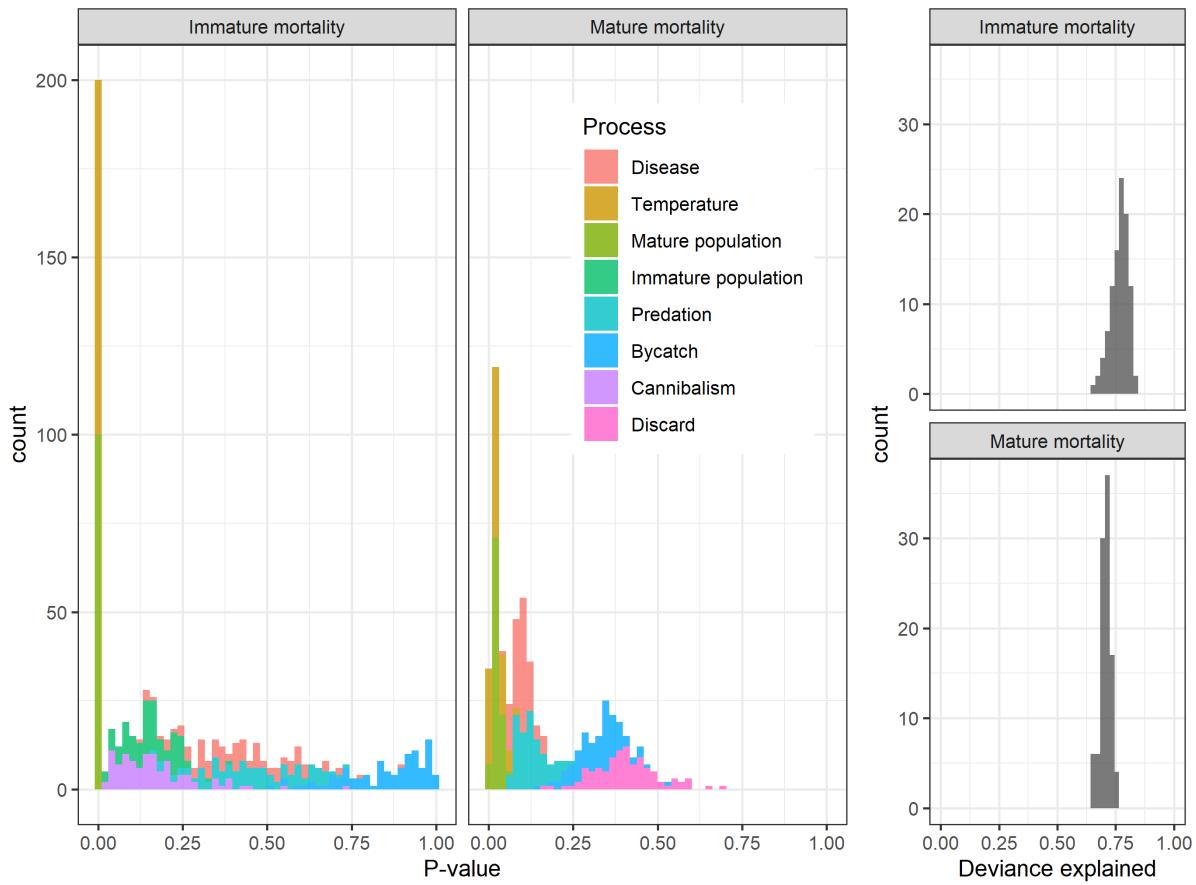


Figure S46: P-values associated with iterations of fitting the GAMs to simulated time series of estimated immature and mature mortality using the covariance matrices estimated in the fitting of the population dynamics model.

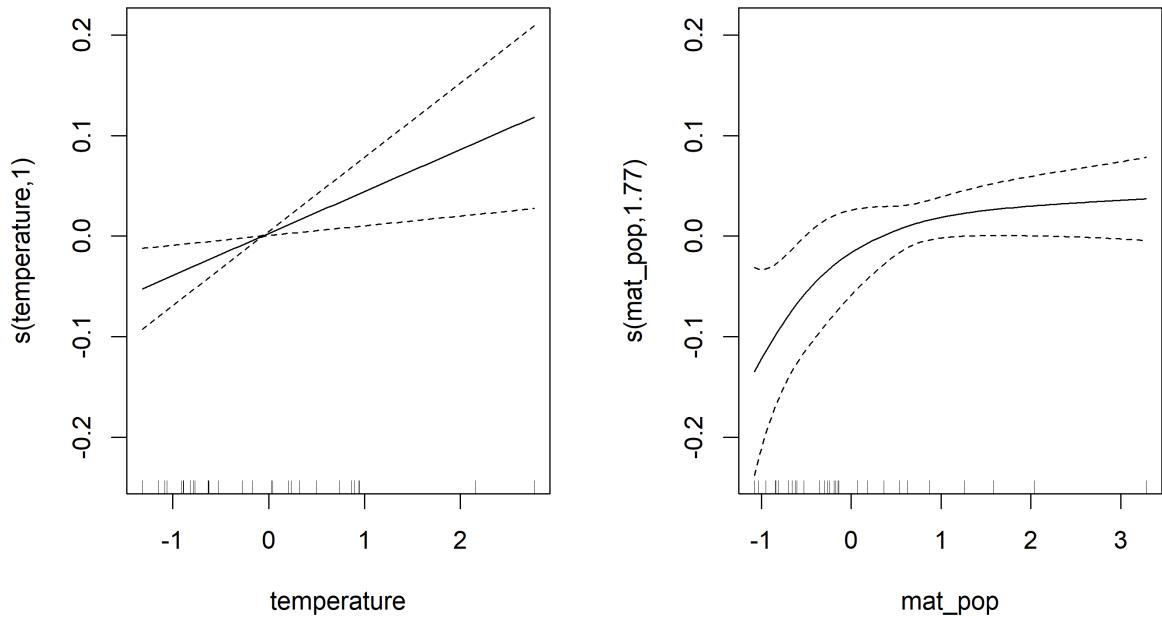


Figure S47: Estimated smooths between immature mortality and temperature occupied and mature population from shape constrained additive models.

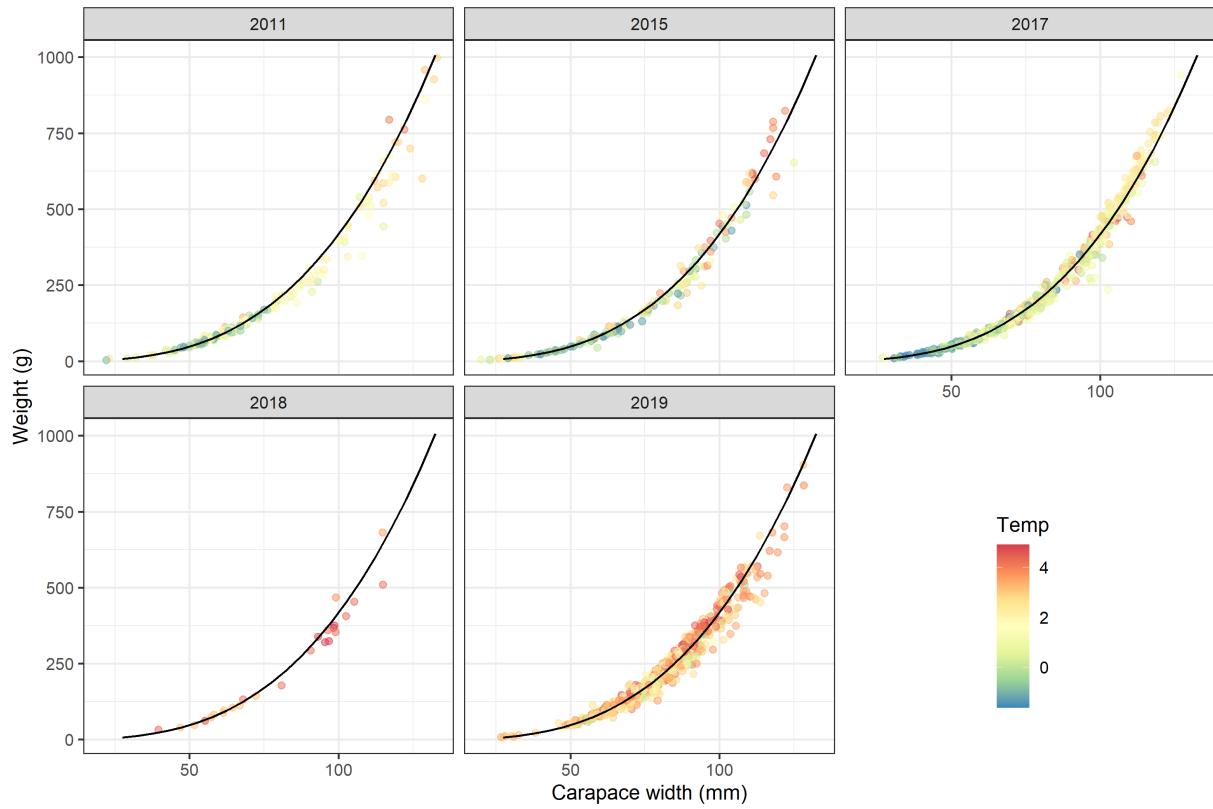


Figure S48: Observed weight at size over time colored by temperature (Celcius) at which the crab was collected.

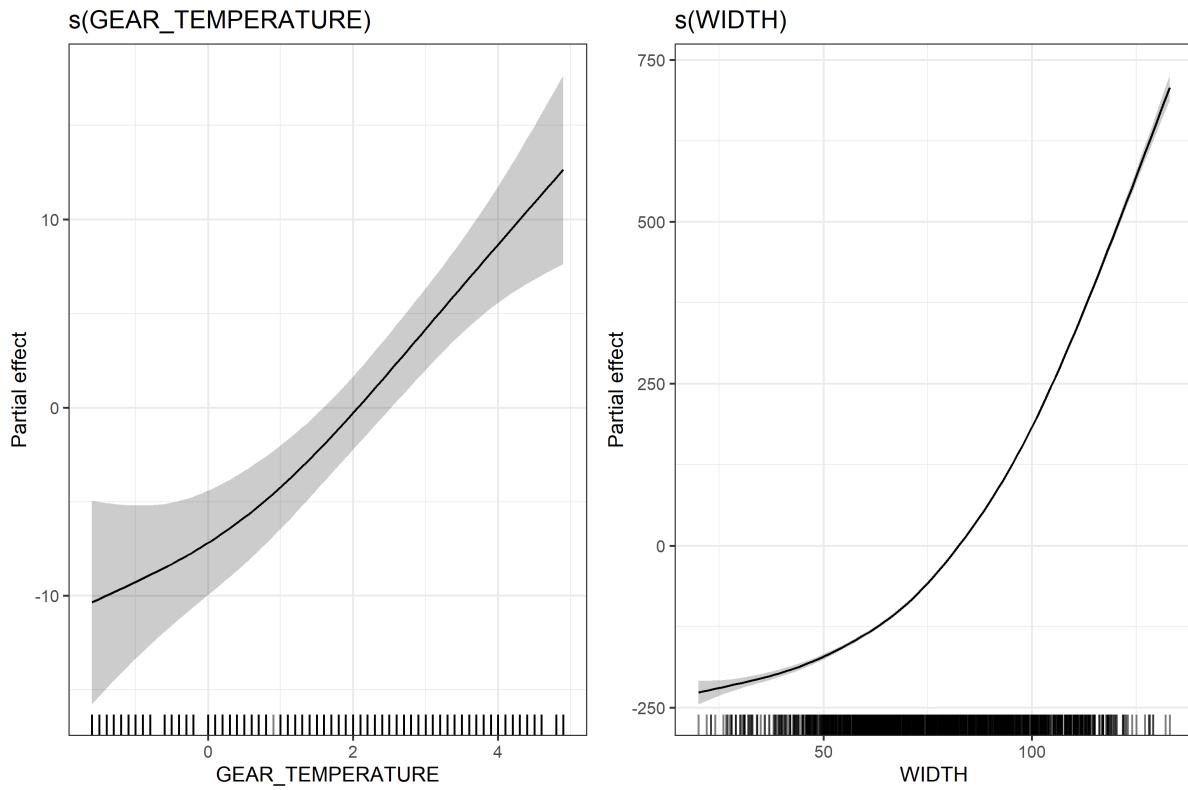


Figure S49: GAM estimated relationships between temperature and carapace width on observed weights of crab.

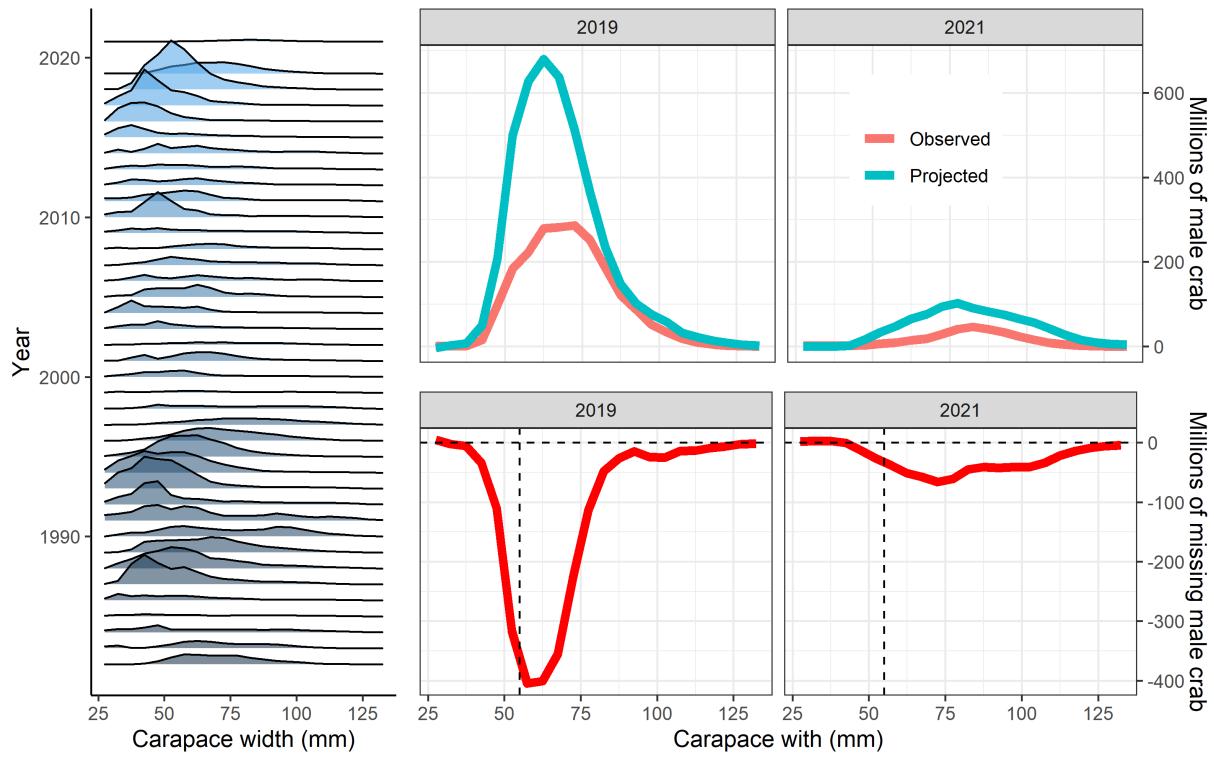


Figure S50: Numbers at size over time of snow crab (left). Observed numbers of crab (red line) in 2019 and 2021 vs. projected numbers of crab from 2018 and 2019 given a mortality equal to 0.27 (the assumed value in the assessment; top left). Numbers of missing crab at size (red line) with the size of crab beneath which cod predate upon (dashed vertical black line).

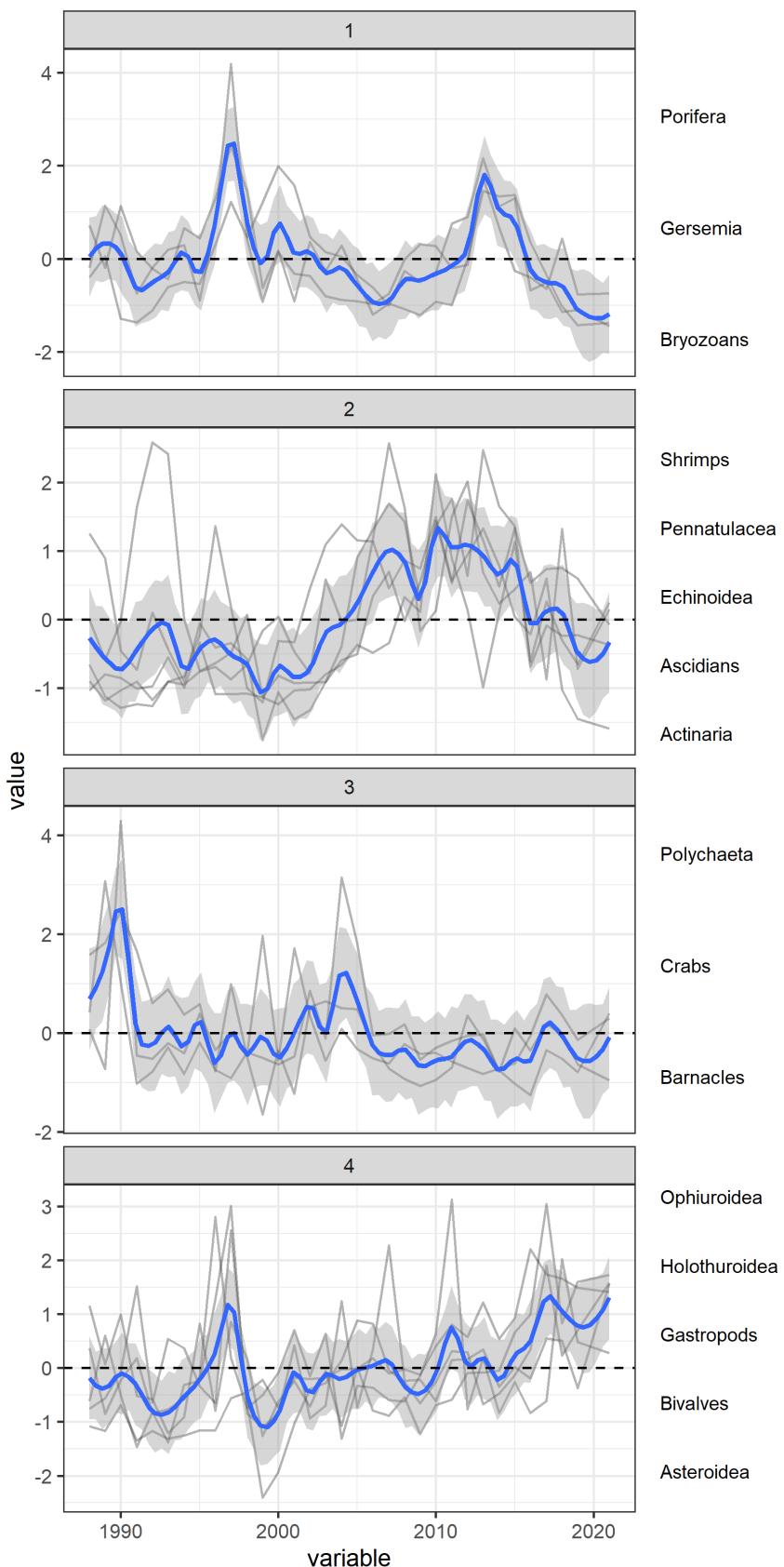


Figure S51: Hierarchical clusters of scaled benthic prey group biomass in the eastern Bering Sea. Blue lines are the fits from a LOESS smoother with a span set to  $0.12^{68}$ . Grey lines in the background are the individual scaled time series of observed prey biomass. Names of the species group included in each cluster are to the right of each figure.

## References and Notes

1. R. Hilborn, R. O. Amoroso, C. M. Anderson, J. K. Baum, T. A. Branch, C. Costello, C. L. de Moor, A. Faraj, D. Hively, O. P. Jensen, H. Kurota, L. R. Little, P. Mace, T. McClanahan, M. C. Melnychuk, C. Minto, G. C. Osio, A. M. Parma, M. Pons, S. Segurado, C. S. Szwalski, J. R. Wilson, Y. Ye, Effective fisheries management instrumental in improving fish stock status. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 2218–2224 (2020).
2. L. A. Copeman, C. H. Ryer, L. B. Eisner, J. M. Nielsen, M. L. Spencer, P. J. Iseri, M. Ottmar, Decreased lipid storage in juvenile Bering Sea crab (*Chionoecetes* spp.) in a warm (2014) compared to a cold (2012) year on the southeastern *Bering Sea*. *Polar Biol.* **44**, 1883–1901 (2021).
3. C. S. Szwalski, “Stock assessment of Eastern Bering Sea snow crab. Stock assessment and fishery evaluation report for the king and tanner crab fisheries of the Bering Sea and Aleutian Islands regions” (North Pacific Fishery Management Council, 2021).
4. I. S. Chernienko, Standardization of landing efficiency of opilio crab in the western Bering Sea by using generalized additive models. *Izvestiya TINRO* **210**, 359–370 (2021).
5. G. R. Hoff, “Results of the 2016 eastern Bering Sea upper continental slope survey of groundfish and invertebrate resources,” NOAA technical memorandum NMFS-AFSC-339 (2016).
6. T. P. Foyle, R. K. O’Dor, R. W. Elner, Energetically defining the thermal limits of the snow crab. *J. Exp. Biol.* **145**, 371–393 (1989).
7. G. M. Lang, P. A. Livingston, “Food habits of key groundfish species in the eastern Bering Sea slope regions,” NOAA technical memorandum NMFS-AFSC-67 (1996).
8. G. A. Lovrich, B. Sainte-Marie, Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura: Majidae), and its potential importance to recruitment. *J. Exp. Mar. Biol. Ecol.* **211**, 225–245 (1997).
9. T. R. Meyers, J. F. Morado, A. K. Sparks, G. H. Bishop, T. Pearson, D. Urban, D. Jackson, Distribution of bitter crab syndrome in Tanner crab (*Chionoecetes bairdi*, *C. opilio*) from the Gulf of Alaska and the Bering Sea. *Dis. Aquat. Organ.* **26**, 221–227 (1996).
10. S. N. Wood, Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Series B Stat. Methodol.* **73**, 3–36 (2011).
11. K. E. Smith, M. T. Burrows, A. J. Hobday, N. G. King, P. J. Moore, A. Sen Gupta, M. S. Thomsen, T. Wernberg, D. A. Smale, Biological impacts of marine heatwaves. *Ann. Rev. Mar. Sci.* **15**, 119–145 (2023).
12. S. J. Barbeaux, K. Holsman, S. Zador, Marine heatwave stress test of ecosystem-based fisheries management in the Gulf of Alaska Pacific cod fishery. *Front. Mar. Sci.* **7**, 703 (2020).

13. C. S. Szuwalski, W. Cheng, R. Foy, A. J. Hermann, A. B. Hollowed, K. Holsman, J. Lee, W. Stockhausen, J. Zheng, Climate change and the future productivity and distribution of crab in the Bering Sea. *ICES J. Mar. Sci.* **78**, 502–515 (2020).
14. E. J. Fedewa, T. M. Jackson, J. Richar, J. L. Gardner, M. A. Litzow, Recent shifts in northern Bering Sea snow crab (*Chionoecetes opilio*) size structure and the potential role of climate-mediated range contraction. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **181–182**, 104878 (2020).
15. B. Garber-Yonts, J. Lee, “SAFE report for the king and tanner crab fisheries of the Gulf of Alaska and Bering Sea/Aleutian Islands Area: Economic status of the BSAI king and tanner crab fisheries off Alaska, 2021” (North Pacific Fishery Management Council, 2021).
16. L. Bellquist, V. Saccomanno, B. X. Semmens, M. Gleason, J. Wilson, The rise in climate change-induced federal fishery disasters in the United States. *PeerJ* **9**, e11186 (2021).
17. NOAA Fisheries, Fisheries of the United States Report (NOAA, 2022); <https://www.fisheries.noaa.gov/foss>.
18. E. C. Siddon, S. G. Zador, G. L. Hunt Jr., Ecological responses to climate perturbations and minimal sea ice in the northern Bering Sea. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **181–182**, 104914 (2020).
19. D. Goethel, D. Hanselman, C. Rodgveller, K. Echave, B. Williams, S. Shotwell, J. Sullivan, P. Hulson, P. Malecha, K. Siwicke, C. Lunsford, “Assessment of the sablefish stock in Alaska. NPFMC Bering Sea, Aleutian Islands and Gulf of Alaska Stock Assessment and Fishery Evaluation report” (North Pacific Fishery Management Council, 2022).
20. Food and Agriculture Organization, *The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation* (Food and Agriculture Organization, 2022); .
21. J. Ianelli, B. Fissel, S. Stienessen, T. Honkalehto, E. Siddo, C. Allen-Akselrud, “Assessment of the walleye pollock stock in the eastern Bering Sea. NPFMC Bering Sea, Aleutian Islands and Gulf of Alaska Stock Assessment and Fishery Evaluation report” (North Pacific Fishery Management Council, 2022).
22. F. Mueter, N. Bond, J. Ianelli, A. Hollowed, Expected declines in recruitment of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea under future climate change. *ICES J. Mar. Sci.* **68**, 1284–1296 (2011).
23. M. Rantanen, A. Y. Karpechko, A. Lipponen, K. Nordling, O. Hyvarinen, K. Ruosteenaja, T. Vihma, A. Laaksonen, The Arctic has warmed nearly four times faster than the globe since 1979. *Commun. Earth Environ.* **3**, 168 (2022).
24. C. S. Szuwalski, A. B. Hollowed, K. K. Holsman, J. N. Ianelli, C. M. Legault, M. C. Melnychuk, D. Ovando, A. E. Punt, Unintended consequences of climate adaptive fisheries management targets. *Fish Fish.* **24**, 439–453 (2023).
25. C. S. Szuwalski, K. Aydin, E. J. Fedewa, B. Garber-Yonts, M. A. Litzow, The collapse of eastern Bering Sea snow crab. Zenodo (2023); <https://zenodo.org/record/8184862>.

26. S. L. Tamone, M. M. Adams, J. M. Dutton, Effect of eyestalk ablation on circulating ecdysteroids in hemolymph of snow crab *Chionoecetes opilio*: Physiological evidence for a terminal molt. *Integr. Comp. Biol.* **45**, 166–171 (2005).
27. D. A. Somerton, K. L. Weinberg, S. E. Goodman, Catchability of snow crab (*Chionoecetes opilio*) by the eastern Bering Sea bottom trawl survey estimated using a catch comparison experiment. *Can. J. Fish. Aquat. Sci.* **70**, 1699–1708 (2013).
28. C. S. Szuwalski, Estimating time-variation in confounded processes in population dynamics modeling: A case study for snow crab in the eastern Bering Sea. *Fish. Res.* **251**, 106298 (2022).
29. O. Hamel, A method for calculating a meta-analytical prior for the natural mortality rate using multiple life history correlates. *ICES J. Mar. Sci.* **72**, 62–69 (2015).
30. G. G. Thompson, Confounding of gear selectivity and natural mortality rate in cases where the former is a nonmonotone function of age. *Can. J. Fish. Aquat. Sci.* **51**, 2654–2664 (1994).
31. K. F. Johnson, C. C. Monnahan, C. R. McGilliard, K. A. Vert-Pre, S. C. Anderson, C. F. Cunningham, F. Hurtado-Ferro, R. R. Licandeo, M. L. Muradian, K. Ono, C. S. Szuwalski, J. L. Valero, A. R. Whitten, A. E. Punt, Time-varying natural mortality in fisheries stock assessment models: Identifying a default approach. *ICES J. Mar. Sci.* **72**, 137–150 (2014).
32. H. Akaike, A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* **19**, 716–723 (1974).
33. M. W. Dorn, C. L. Barnes, Time-varying predation as a modifier of constant natural mortality for Gulf of Alaska walleye pollock. *Fish. Res.* **254**, 106391 (2022).
34. L. S. Zacher, J. I. Richar, E. J. Fedewa, E. R. Ryznar, M. A. Litzow, “The 2022 Eastern Bering Sea continental shelf trawl survey: Results for commercial crab species,” NOAA technical memorandum NMFS-AFSC (2022); [https://apps.afsc.fisheries.noaa.gov/plan\\_team/resources/draft\\_ebs\\_crab\\_tech\\_memo\\_2022.pdf](https://apps.afsc.fisheries.noaa.gov/plan_team/resources/draft_ebs_crab_tech_memo_2022.pdf).
35. Alaska Fisheries Information Network (AKFIN), 2022; <https://akfin.psmfc.org>.
36. B. Ernst, J. M. L. Orensanz, D. A. Armstrong, Spatial dynamics of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. *Can. J. Fish. Aquat. Sci.* **62**, 250–268 (2005).
37. C. Parada, D. A. Armstrong, B. Ernst, S. Hinckley, J. M. Orensanz, Spatial dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea—Putting together the pieces of the puzzle. *Bull. Mar. Sci.* **86**, 413–437 (2010).
38. F. J. Mueter, M. A. Litzow, Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecol. Appl.* **18**, 309–320 (2008).
39. M. Dionne, B. Sainte-Marie, E. Bourget, D. Gilbert, Distribution and habitat selection of early benthic stages of snow crab (*Chionoecetes opilio*). *Mar. Ecol. Prog. Ser.* **259**, 117–128 (2003).

40. K. K. Holsman, K. Aydin, Comparative methods for evaluating climate change impacts on the foraging ecology of Alaskan groundfish. *Mar. Ecol. Prog. Ser.* **521**, 217–235 (2015).
41. P. A. Livingston, K. Aydin, T. W. Buckley, G. M. Lang, M.-S. Yang, B. S. Miller, Quantifying food web interactions in the North Pacific—a data-based approach. *Environ. Biol. Fishes* **100**, 443–470 (2017).
42. J. Burgos, B. Ernst, D. Armstrong, J. M. Orensanz, Fluctuations in range and abundance of snow crab from the eastern Bering Sea: What role for Pacific cod predation? *Bull. Mar. Sci.* **89**, 57–81 (2013).
43. M. Kleiber, Body size and metabolic rate. *Physiol. Rev.* **27**, 511–541 (1947).
44. D. Hardy, J. D. Dutil, G. Godbout, J. Munro, Survival and condition of hard shell male adult snow crabs (*Chionoecetes opilio*) during fasting at different temperatures. *Aquaculture* **189**, 259–275 (2000).
45. M. Zimmermann, C. B. Dew, B. A. Malley, History of Alaska red king crab, *Paralithodes camtschaticus*, bottom trawl surveys, 1940–1961. *Mar. Fish. Rev.* **71**, 1–22 (2009).