

1 Appendix B: Canaries of the Arctic: the collapse of eastern Bering
2 Sea snow crab

3 Cody Szuwalski (and others to come)

4 Snow crab are an iconic species the Bering Sea that support an economically important fishery and undergo
5 extensive monitoring and management. However, since 2018 more than 10 billion snow crab have disappeared
6 from the Bering Sea shelf and the population collapsed to historical lows in 2021. We link this collapse to
7 a marine heatwave that occurred in the Bering Sea during 2018 and 2019. Calculated caloric requirements
8 and observed body condition suggests that starvation may have played a role in the collapse. Fisheries
9 disaster funds were requested in 2022 after allowable catches in the fisheries were slashed by ~90% in 2021
10 and short-term prospects for snow crab in the Bering Sea are grim. The collapse of snow crab foreshadows
11 climate-related fisheries management problems that will be more frequently faced around the globe. Losing
12 a frame of reference for future ecosystems as environmental conditions move beyond historical observations
13 shifts our management paradigm from predictive to reactive. New managements paradigms will be needed
14 to face this challenge.

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18 THIS IS A DRAFT MANUSCRIPT INTENDED FOR SUBMISSION TO A PEER-REVIEWED JOURNAL

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21 ALL CONCLUSIONS ARE PRELIMINARY

22 Introduction

23 Snow crab are one of the most abundant species in the benthic ecosystem of the eastern Bering Sea and have
24 supported an iconic fishery valued at over US\$250 million that is the focus of “Deadliest catch”, a widely
25 viewed reality television show. The implementation of quota-based fisheries management in 2005 has made
26 the fishery less ‘deadly’ (NPFMC, 2010) and fisheries management in Alaska is considered to be some of
27 the most effective in the world (Hilborn et al., 2021). Snow crab are distributed widely over the Bering
28 Sea shelf (Figure 1a) and yearly bottom trawl surveys monitor the size and number of crab in the ocean.
29 Myriad field and laboratory studies aimed at understanding population processes like growth and maturity
30 have been performed (e.g. Copeman et al., 2021), but in spite of this attention and effort, the stock collapsed
31 unexpectedly in 2021.

32 The collapse in 2021 occurred three years after the observed abundance of snow crab was at historical
33 highs (Figure 1c). Groups of crab of similar sizes are called ‘pseudocohorts’ because true cohorts cannot be
34 identified as a result of difficulties in aging crab associated with the loss of the hard body parts during the
35 molting process. The largest pseudocohort on record was observed in the summer survey beginning in 2015
36 and unexpectedly declined by roughly half from 2018 to 2019 (Figure 1d). The survey was cancelled in 2020
37 because of the coronavirus pandemic, but the 2021 survey found the fewest snow crab on the eastern Bering
38 Sea shelf since the survey began in 1975. More than 10 billion crab went missing from the eastern Bering
39 Sea shelf from 2018 to 2021 (Szuwalski, 2021).

40 Hypotheses to explain the disappearance of these crab fall under two categories: either the crab are still alive
41 but the survey did not see them or the crab have died. It is possible the crab are in the eastern Bering Sea,
42 but were poorly captured by the most recent surveys. If this were the case, one would expect estimates for
43 other similar species like Tanner crab to have declined unexpectedly, but the population trends for Tanner
44 crab increased (figures S1). Movement to the northern Bering Sea could account for declines in the eastern
45 Bering Sea, but surveys in the northern Bering Sea did not find crab in the quantities or of the correct sizes
46 to explain declines in the south (Figure 1a). Movement west into Russian waters is another possibility, but
47 Russian scientists reported declines in catch per unit effort in 2020 (Chernienko, 2021), which one might not
48 expect if crab from Alaska emigrated. Finally, it is possible that the crab moved into deeper waters on the
49 Bering Sea slope. High fishery catch per unit effort in deeper waters during the 2021 fishery supports this
50 possibility to some extent, but the amount of available habitat is less than 10% that on the shelf (figures S2)
51 and fishery catch per unit effort from 2022 were the lowest on record (figure S3). Consequently, it is unlikely
52 that all of the missing crab from the shelf are on the slope. Given these observations, although movement
53 off of the shelf could have played some role in the decline, mortality is a likely culprit for the bulk of the
54 collapse.

55 Mortality could be affected via several pathways. Snow crab are generally cold-water loving, but they can
56 function in waters up to 12 degrees in the laboratory (Foyle et al., 1989). An intense marine heatwave
57 occurred in the Bering Sea during 2018 and 2019 and the ‘cold pool’ (a mass of water <2 degrees C on the
58 sea floor with which juvenile snow crab are associated) disappeared during this period (Figure 1b). While
59 not fatal, the resulting bottom temperatures could affect metabolic costs and alter intra- and inter-specific
60 interactions. Smaller crab are a main component of the diet of Pacific cod in the Bering Sea (Lang and
61 Livingston, 1996) and recent changes in the distribution and abundance of cod and crab has resulted in
62 increased consumption. Removals from the snow crab fishery and incidental mortality in fisheries for other
63 species in the Bering Sea also may also impact the dynamics of snow crab. Larger snow crab are known
64 to cannibalize smaller snow crab and cannibalism has been suggested as an important driver of population
65 dynamics in eastern Canadian populations (Lovrich et al., 1997). Finally, bitter crab syndrome, a fatal
66 disease resulting from infection by a dinoflagellate (Meyers et al. 1996), has been observed more frequently
67 in the summer survey in the last several years and is generally associated with warmer conditions and high
68 densities of immature crab.

69 To understand the recent collapse, we first attempt to understand the historical variability in mortality. We
70 fit a population dynamics model to the abundance and size composition data for male crab and estimated
71 recruitment (small crab entering the population) and a maturity- and year-specific total mortality. ‘Total
72 mortality’ represents the fraction of crab dying in a given year due to any cause. We then collated maturity-

73 specific time series of potential stressors from 1991 to 2019 and used them in generalized additive models
74 (GAMs; Woods, 2011) to predict total mortality estimated from the population dynamics models (see SI for
75 detailed methodology, sensitivities, and simulation testing).

76 The population dynamics model fit the indices of abundance and size composition data from the survey
77 well, which is not unexpected, given the flexibility of the model (Figure 2a & b). Estimated mortality was
78 higher and more varied for mature crab than for immature crab and estimated mortalities in 2018 and
79 2019 were the some of the highest for both immature and mature crab in the time series. We simulated
80 snow crab populations with time-variation in mortality to understand the ability of our population dynamics
81 model to estimate these quantities with the available data. The correlation between estimated mortality and
82 simulated mortality were high which suggests that analyses relating estimates of mortality and environmental
83 covariates are justifiable (see SI for details). GAMs fit to estimated immature and mature mortality both
84 returned at least one significant relationship with environmental stressors and explained ~72% and ~66%
85 of the variability, respectively (Figure 2c). Higher temperatures and higher densities of mature crab were
86 associated with higher mortality for both immature and mature crab. These relationships were robust to
87 leave-one-out-cross validation and the deviance explained was ‘significant’ under randomization trials (see
88 SI).

89 Assessing the predictive skill of a model is an important check on over-fitting and relevant to providing
90 management advice. After an ecologically damaging and economically costly collapse, it is natural to ask
91 if we could have foreseen the collapse. To explore this question, we excluded 1, 2, and 3 years of data
92 from the end of the time series, refit the models, then tried to predict the last years of mortality with the
93 covariates from those years. The model for immature mortality contained enough information in 2016 to
94 forecast an increase in mortality, but never was able to reach the magnitude of the estimated mortality in
95 2019 (Figure 2c). The model for mature mortality performed similarly, forecasting an increase in mortality
96 over the projection period, but was not able to reach the estimated mortalities until the most recent data
97 was in the model. This suggests that the circumstances underpinning the recent collapse were unprecedented
98 in the Bering Sea in recent history.

99 The collapse of eastern Bering Sea snow crab appears to be one of the largest reported losses of marine
100 macrofauna to marine heatwaves globally, exacerbated by the record number of snow crab in the system.
101 Temperatures and density of mature crab were the most extreme covariates in 2018 and 2019. However,
102 temperature and density alone are not a very satisfying explanation for what happened to the crab because
103 the physiological thermal limits for snow crab far exceed the observed temperatures (Foyle et al., 1998).
104 Temperature dependent caloric requirements are a potential explanation to relate temperature to mortality.
105 Foyle et al. (1998) showed the caloric requirements for snow crab in the lab nearly double from 0 degrees
106 to 3 degrees, which is roughly the change experienced by immature crab from 2017 to 2018 (Figure 3).
107 Extrapolating the caloric requirements based on temperature occupied, abundance of crab at size, and
108 weight at size suggests that the caloric requirements for snow crab in the eastern Bering Sea during 2018
109 quadrupled from 2017 and were double the previous maximum value in 1998. The impact of increased caloric
110 demands can also be seen in the observed weight at size. A 75 mm carapace width crab in 2018 weighed on
111 average 156 grams and was ~25 grams lighter (~15% of its bodyweight) than a crab in 2017 of the same size
112 in the same temperature waters (Figure 3). Given this information, starvation likely played a role in the
113 disappearance of the ~10 billion snow crab, similar to the marine-heatwave related collapse of Pacific cod in
114 the Gulf of Alaska in 2016 (Barbeaux et al., 2020).

115 Snow crab previously collapsed in the late 1990s, but the collapse arose from a lack of recruitment, not a
116 sudden mortality event. Snow crab recruitment has been linked to changes in the Arctic Oscillation and sea
117 ice (Szuwalski et al., 2020). Recent projections of recruitment suggest snow crab abundances will decline in
118 the future as sea ice disappears from the eastern Bering Sea (Szuwalski et al., 2021). However, these declines
119 were projected for at least twenty years from now. Given the recent collapse, the short-term future of snow
120 crab in the eastern Bering Sea is precariously uncertain. Long-term the northern Bering Sea is a prospective
121 climate refugia for snow crab (and potentially a fishery; Mullowney, in review), but the possibility of a fishery
122 rests on the uncertain probability of crab growing to a larger size in the north and the currents retaining
123 pelagic larvae released in the northern Bering Sea.

124 In 2021, 59 boats fished for snow crab and brought \$219 million (ex-vessel) into fishing communities (Garber-

125 Yonts, 2022). The disappearance of snow crab will be a staggering blow to the functioning of some com-
126 munities in rural Alaska like St. Paul, which relies strongly on the revenue derived from the capture and
127 processing of snow crab to support the functioning of local communities. The Magnuson-Stevens Act includes
128 provisions for fisheries disaster assistance which were designed to provide economic support for communities
129 facing hardship as a result of collapsed fisheries. The number of applications in the U.S. has been increasing
130 in recent years (Bellquist et al., 2021) and an application for snow crab was received in early 2022. These
131 funds are a boon in the medium-term, but can take years from disaster to dispersal. Consequently, Alaskan
132 crabbers face an uncertain short-term future as the disaster funds may not arrive in time to forestall the
133 bankruptcy of long-standing family businesses.

134 Beyond the fishery for snow crab, Alaskan fisheries are some of the most productive in the world, producing
135 5.27 billion tons of seafood in 2021 valued at \$1.9 billion (NOAA FOSS, 2022). When snow crab populations
136 declined in 1999, the Bering Sea walleye pollock population (which supports the largest fishery in the Bering
137 Sea and one of the largest in the world, FAO, 2022) also declined shortly after (Figure 4). This relationship
138 is captured by the significant correlation between the time series of pollock and snow crab abundance at a
139 lag of 1 year (Figure 4d). While this correlation is suggestive, it is ultimately uncertain how the massive loss
140 of crab will affect the benthic ecosystem and the fisheries dependent upon it. However, it is virtually certain
141 that the benthic community in the eastern Bering Sea during not-too-distant future will look different than
142 today's given the rapid pace of warming (Rantanen et al., 2022).

143 Overfishing has historically been the largest threat to global fisheries, but, in many parts of the world, this
144 problem has been solved (Hilborn et al., 2022). Climate change is the next existential crisis for fisheries,
145 and snow crab is a prime example for how quickly the outlook can change for a population. In 2018, catches
146 were projected to increase to levels not seen in decades. Three years later, the population had collapsed.
147 Our current management tools base projected sustainable yields on the historical dynamics of a population.
148 However, projections based on assumptions relying on historical dynamics are not reliable when the future
149 of a region will not resemble the past. Beyond reconsidering how allowable catches are calculated, the
150 practical matters of efficient disaster response, implementing management institutions that allow fishers to
151 pursue diverse portfolios of species, and support for the development of alternative marine-based livelihoods
152 (e.g. mariculture) need close attention from management and stakeholders. The Bering Sea is on the front
153 lines of climate-driven ecosystem change and the problems currently faced in the Bering Sea foreshadow the
154 problems that will need to be confronted globally.

155 **Acknowledgments**

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157 **Supplementary materials**

158 The github repository including the code used to perform the analysis can be found at: https://github.com/szuwalski/snow_down.
159

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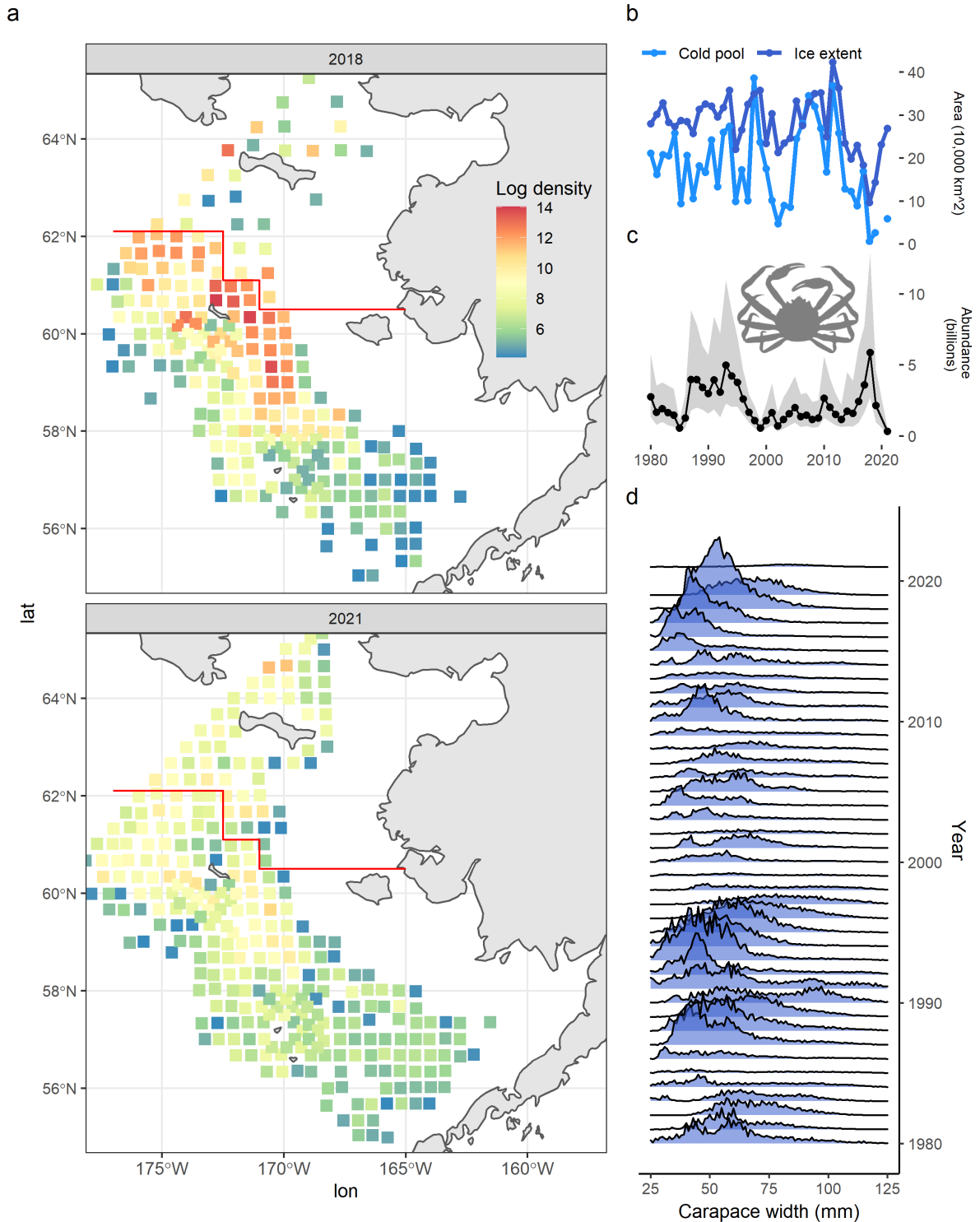
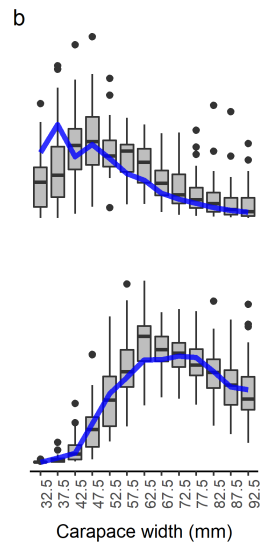
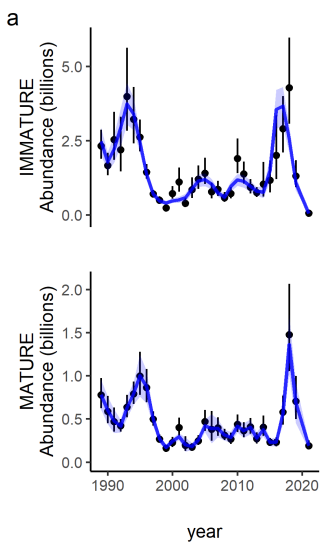


Figure 1: The collapse of snow crab in the eastern Bering Sea. Snow crab are widely distributed on the eastern Bering Sea shelf (a, each square represents a survey tow with snow crab present) and densities of crab were an order of magnitude lower in 2021 compared to 2018 (a). Changes in ice extent and the resulting cold pool (b) influence the population dynamics (c) of snow crab (only male abundance is plotted). The collapse of crab was not size dependent; crab of all sizes disappeared from 2018 to 2021 (d shows the relative numbers at size at crab observed in the NMFS survey over time).

Population Dynamics



Generalized Additive Models

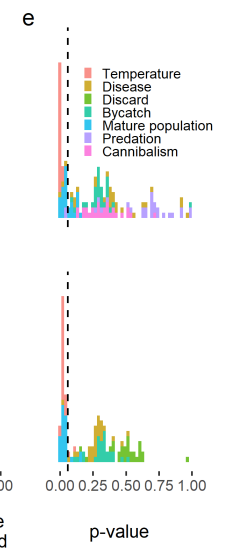
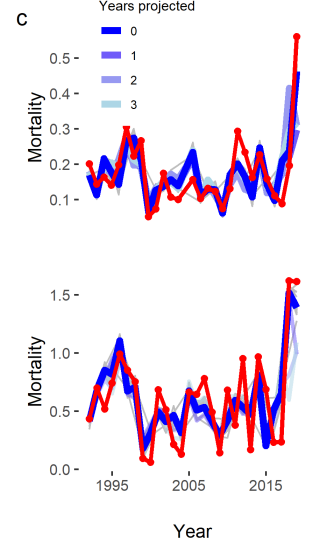


Figure 2: Population dynamics model fits to the data (abundance and confidence intervals (a), size composition data (b)). Fits (c; in blue) to estimated mortality (c; in red) from GAMs with the deviance explained (d) and the significance of covariates (e) resulting from replicates over leave-one out cross validation.

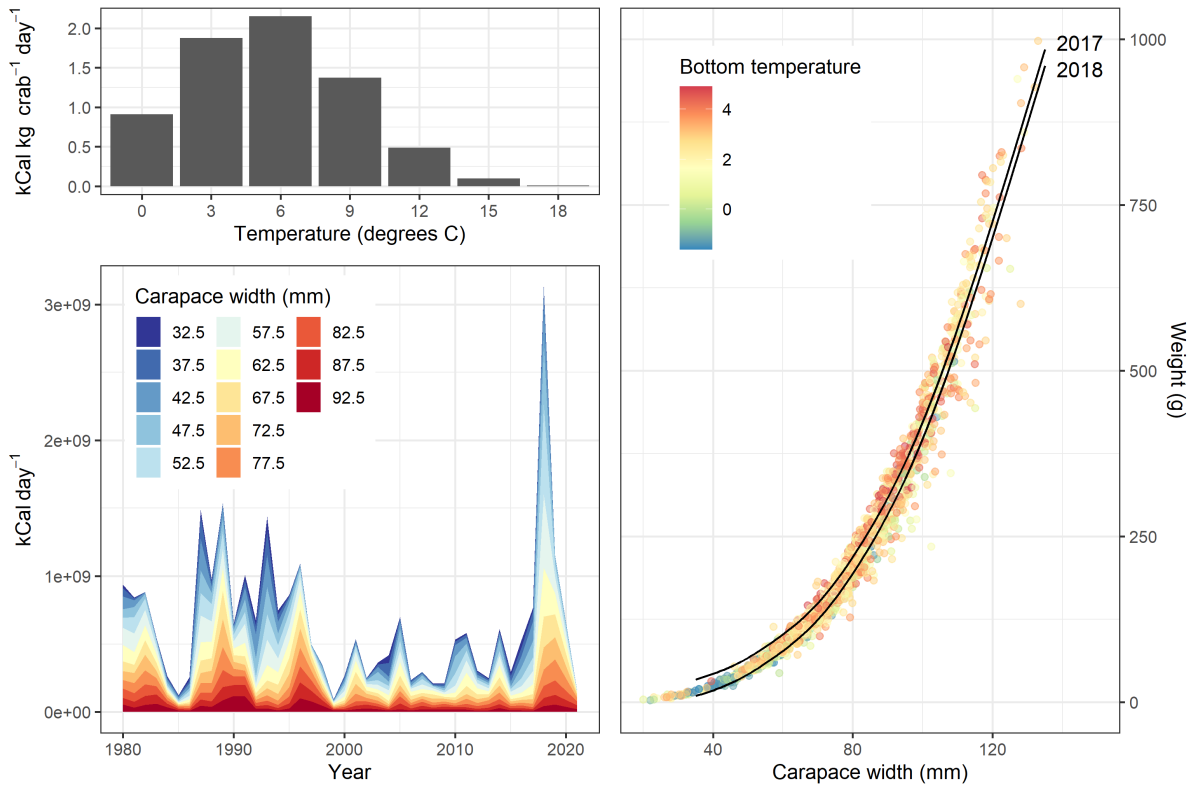


Figure 3: Impact of temperature on caloric requirements for snow crab in the lab (a; reproduced from Foyle et al., 1998), the extrapolated caloric requirements for crab in the eastern Bering Sea based on temperature, abundance at size, and weight at size (b), and the observed weight at size colored by the temperature at which the crab was collected (c). The lines represent the relationship between weight at size in 2017 and 2018 while holding temperature at 1 degree.

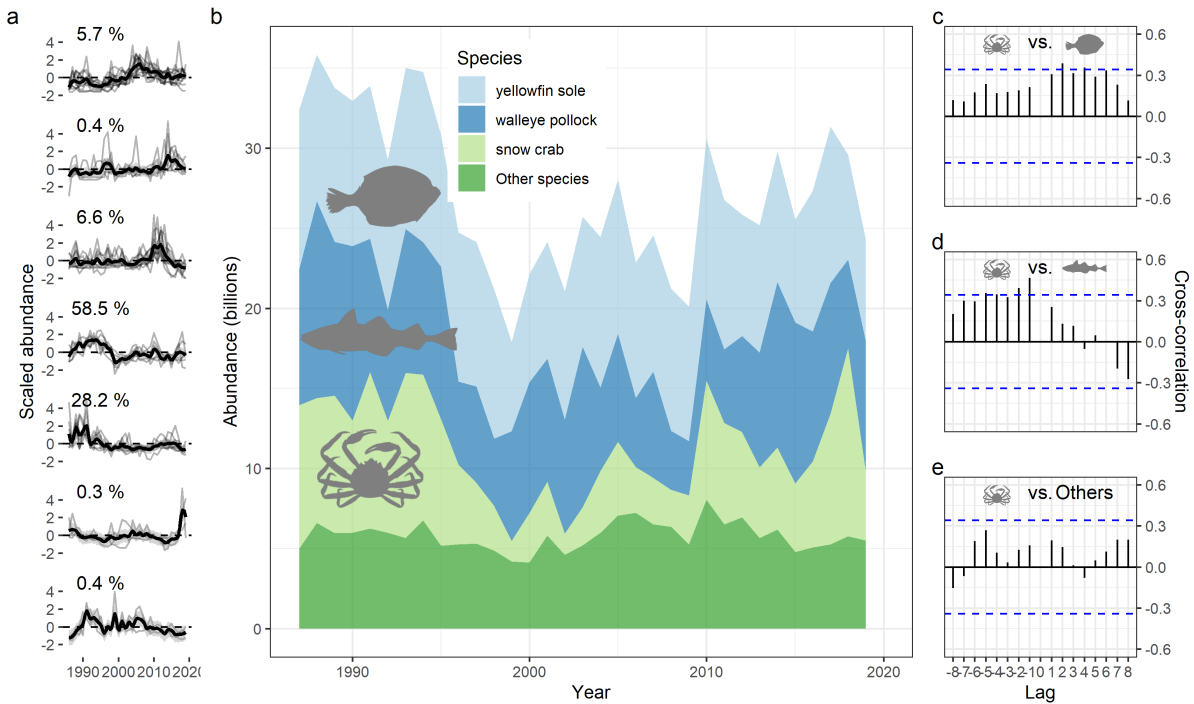


Figure 4: Time-series of scaled abundances of animals captured in the NMFS summer bottom trawl survey clustered using hierarchical clustering (a; 55 species represented, percentage in the top left of the panel represents the average proportion of the total abundance in that cluster) and total abundances over time for the three most abundance species in the bottom trawl survey and all 'other species' combined (b). Panels c-e are the cross-correlation between the time series of abundance for snow crab against yellowfin sole, walleye pollock, and other species, respectively.