

1 Estimating time-variation in confounded processes in population
2 dynamics modeling: a case study for snow crab in the eastern
3 Bering Sea

4 Cody Szuwalski

5 Population dynamics models used to provide management advice for harvested natural resources often es-
6 timate population processes that can be mutually confounded. These processes (e.g., natural mortality
7 (M) and catchability (q)) are often assumed to be time-invariant, but this assumption can be violated in
8 real populations. Not allowing for time-variation in these processes can result in retrospective patterns in
9 estimated biomass, which can result in errors in management advice. Allowing for time-variation in these
10 processes can also result in errors in management advice if the estimated time-variation does not reflect the
11 true underlying variation. Here I present a population dynamics model for snow crab in the eastern Bering
12 Sea that tests different combinations of implementation of time-variation in M and q . The North Pacific
13 Fisheries Management Council did not adopt any of the models with time-variation in M or q for man-
14 agement because the estimated variability in M and q was difficult to explain with any known mechanism
15 and management advice differed by nearly an order of magnitude among models. The large differences in
16 management advice reported here underscore the importance of evidence-based approaches to incorporating
17 time-variation in population processes into stock assessment models.

18 Introduction

19 Modeling the dynamics of populations often requires making simplifying assumptions to produce tenable
20 models. For example, in fisheries stock assessments, population processes like natural mortality (M), catch-
21 ability (q), growth, and maturity are often assumed to be time-invariant. However, these assumptions have
22 been shown to be false for some populations. For example, Wilberg et al. (2009) collated published evidence
23 for changes in catchability for harvested marine population, Stawitz et al. (2019) demonstrated considerable
24 variability in growth for stocks in the Bering Sea, and Jacobsen and Essington (2018) cataloged changes in
25 natural mortality for forage fish in European waters.

26 Addressing the potential that other confounded processes are not driving observed changes in a stock is a
27 key concern when estimating time-variation in stock assessment. Similar changes in the observed indices of
28 abundance can be caused by changes in natural mortality, selectivity, growth, or catchability (e.g., Thompson,
29 1994). For example, a decline in biomass in the terminal year of the time series can arise from increased
30 natural mortality, decreased selectivity or catchability, or decreases in growth. This confounding can lead
31 to the dilemma of ‘Kill them or hide them?’ when assessing stocks in which there are unexpected declines
32 (Taylor and Methot, 2013). Data to distinguish between mortality events and changes in selectivity are often
33 difficult to procure and, even when the data are possible to collect, may arrive after the point in time at
34 which they are needed to establish management advice (e.g., the next year’s survey data). In spite of this,
35 the analyst must make modeling decisions about how to reconcile changes in observed abundance or biomass
36 to provide management advice.

37 Given the above issues, population dynamics models used to manage harvested natural resources often seek
38 to strike a balance between simplicity and complexity in modeling assumptions that appropriately captures
39 the processes important in determining sustainable harvests (e.g., natural mortality, growth, selectivity,
40 catchability, and maturity) while respecting the information content in the data. In general, three pieces of
41 information are needed in harvest control rules that produce catch recommendations: biomass at the time
42 of the next fishery, a target biomass, and a target fishing mortality. Broadly speaking, these pieces represent
43 the current status of a fishery, the target status for a fishery, and the pathway for how to achieve the target
44 from the current situation. Oftentimes the biomass and fishing mortality targets are based on maximum
45 sustainable yield calculations (e.g., Schaefer, 1954) or proxies thereof (e.g Clark, 1991).

46 Each of these pieces of information can be influenced by the assumptions about population processes made
47 while developing a population dynamics model. Assuming time-invariance in the population processes that
48 influence estimates of current biomass when those processes are actually varying can produce retrospective
49 patterns and lead to ineffective management advice (e.g., NOAA, 2009). Assuming time-invariance in the
50 population processes that determine the management targets for biomass and fishing mortality may be
51 reasonable if the forcing of these processes is stationary because the targets should represent the mean state
52 of the system. However, if the environmental forcing of these processes is non-stationary (i.e. the mean
53 changes over time), changes in population processes result in changes in management quantities (Thorson
54 et al. 2015) and decisions must be made about the time period used as a reference to calculate management
55 targets (NPFMC, 2007).

56 Snow crab in the eastern Bering Sea is one such stock that appears to have time-variation in some population
57 processes (e.g., natural mortality in Murphy et al. 2018; catchability in Somerton et al. 2013) and models
58 have been proposed for other stocks of snow crab that include time-varying M (Shibata et al., 2021). The
59 eastern Bering Sea population is at least at risk of non-stationarity in some population processes (particularly
60 those related to ice extent like recruitment; Szuwalski et al., 2020). Consequently, we use it here as a case
61 study to explore the potential to estimate time-variation in confounded population processes.

62 The snow crab fishery has been managed with individual transferable quotas since 2005 and retains large male
63 crab with carapace width greater than 101 mm (Figure 1). Catches were highest in the 1990s, after which
64 the stock biomass declined sharply and the stock was declared overfished in 1999. The stock was declared
65 ‘rebuilt’ in 2011 once the estimated biomass exceeded the biomass management target. The National Marine
66 Fishery Services (NMFS) summer trawl survey is a key information source in the stock assessment for snow
67 crab. Crab cannot be aged, so true cohorts are not known, however groups of crab of similar size clearly

68 move through the population and are dubbed ‘pseudocohorts’. Large ‘pseudocohorts’ have appeared in the
69 survey three times since 1982 (Figure 1 and Figure 2).

70 The most recent large pseudocohort was spawned around 2010 and first selected by the survey gear in 2015
71 (Szuwalski et al., 2020). By 2018, it was the largest pseudocohort ever observed in the eastern Bering Sea.
72 However, in 2019, it was much smaller than expected given estimated growth, natural mortality, and fishing
73 removals (Figure 2). This strongly implies time-variation in some population process and catchability or
74 natural mortality are key suspects given previous research. However, there are few data to decisively indicate
75 which process is varying over time. No survey was performed in 2020 as a result of the coronavirus pandemic,
76 so the managing body was in the unprecedented position of setting the overfishing level (i.e. the level of catch
77 beyond which overfishing would occur, which is used to set allowable biological catches) in a year with no
78 survey data and in the context of a large drop in the previous year of survey data that could be attributed
79 to changes in either natural mortality or catchability.

80 Here I present iterations of the assessment method used for snow crab that incorporate time-variation in
81 natural mortality and/or catchability. I then compare the resulting fits to the data, evaluate the character and
82 credibility of the estimated time-variation in q and M , and examine the knock-on effects in other confounded
83 processes like maturity and recruitment. I conclude by presenting the differences in management-related
84 quantities (e.g., $F_{35\%}$ and $B_{35\%}$), summarizing the discussion the management body held concerning these
85 models, and discussing potential paths forward.

86 Methods

87 The integrated size-structured model currently used (referred to here as the ‘status quo’ model) was developed
88 by Turnock (2015) following Fournier and Archibald’s (1982) methods, with many similarities to Methot
89 (1990). The population dynamics in the status quo model tracks the number of crab of sex s , maturity
90 state m , during year y at width w , $N_{s,m,y,w}$. A terminal molt occurs in which crab move from an immature
91 to a mature state, after which no further molting occurs. The mid-points of the size bins tracked in the
92 model span from 27.5 to 132.5 mm carapace width, with 5 mm size classes. Parameters estimated within the
93 assessment include those associated with recruitment, natural mortality (subject to a fairly informative prior),
94 fishing mortality, selectivity (fishery and survey), survey catchability, and probability of having undergone
95 terminal molt. Weight at size, discard mortality, bycatch mortality, and parameters associated with the
96 variance in growth and proportion of recruitment allocated to size bin were estimated outside of the model
97 or specified. Growth parameters were estimated outside of the model based on measurements of pre-molt
98 and post-molt carapace width for crab captured in the wild just prior to molting. Survey biomass indices
99 and size-composition data, directed fishery biomass and size-composition data, and bycatch biomass and
100 size-composition data were fit to within the assessment. The assessment spans the years 1982 to 2020. See
101 appendix A for a complete description of the population dynamics and model code is available on a github
102 repository linked at the end of this manuscript.

103 The output of three models are compared to the status quo here: “Vary M ”, “Vary q ”, and “Vary both”. Each
104 of these models builds on the status quo model and alters the way in which natural mortality (“Vary M ”),
105 catchability (“Vary q ”), or both processes (“Vary both”) are modeled. “Vary M ” adds a vector of deviations
106 to the existing estimated parameters for mature natural mortality of both sexes (i.e. a ‘dev_vector’ in
107 AutoDifferentiating Model Builder; Fournier et al., 2012). The vector of deviations includes an additional
108 parameter for each year included in the assessment (1982-2020) for each sex. “Vary q ” estimates a catchability
109 parameter for each year from 1989-2020 for each sex. The estimated vectors of q are bounded by 0.2 and 1.0
110 based information from experimental net efficiency work for Bering Sea snow crab that suggests catchability
111 should be within this range (Somerton et al., 2013). “Vary both” combines these changes into a single model.
112 A smoothing penalty is added to the negative log likelihood of each model to facilitate model convergence.
113 The smoothing penalty is the squared norm of the second difference of each vector of additionally estimated
114 parameters multiplied by a user-defined weighting factor. The weights for the smoothing penalties were
115 chosen by trial and error, with the aim of making them as small as possible while still avoiding convergence
116 issues.

117 Retrospective analyses were performed in which the terminal year of data was removed sequentially from the
 118 model fitting, then estimated management quantities (e.g., mature male biomass [MMB]) were compared
 119 between the model with the complete data set (i.e. 1982-2020) and models with successive ‘peels’ of the data
 120 to identify retrospective patterns. A retrospective pattern is a consistent directional change in assessment
 121 estimates of management quantities in a given year when additional years of data are added to an assessment.
 122 Mohn’s rho (which computes the average difference between the reference case and the peels over the period
 123 of retrospective analysis; Mohn, 1999) was calculated for each model to quantify the retrospective patterns
 124 in the estimate of the terminal year of biomass.

125 The overfishing level (OFL) is the level of catch beyond which overfishing would be deemed to occur in a given
 126 year. The OFL is one of the key pieces of management advice that arises from the assessment and serves
 127 as the starting point for specifying an ‘acceptable biological catch’, which constrains removals in the fishery.
 128 The OFL was calculated using spawner-per-recruit proxies for biomass and fishing mortality reference points
 129 (e.g., Clark, 1991) and a sloped control rule. After fitting the assessment model to the data, the model was
 130 projected forward 100 years using the estimated parameters under no exploitation and constant recruitment
 131 to determine ‘unfished’ MMB-per-recruit. For models in which time-variation was implemented, the average
 132 of the final seven years of the process was used in projections. The bisection method was used iteratively
 133 to identify a fishing mortality that reduced the MMB-per-recruit to 35% of the unfished level (i.e. $F_{35\%}$ and
 134 $B_{35\%}$). Calculations of $F_{35\%}$ were made under the assumption that bycatch fishing mortality was equal to
 135 the estimated average value.

136 Calculated values of $F_{35\%}$ and $B_{35\%}$ were used in conjunction with a sloped control rule to adjust the
 137 proportion of $F_{35\%}$ that is applied based on the status of the population relative to $B_{35\%}$ (Amendment 24,
 138 NMFS; NPFMC, 2007).

$$F_{OFL} = \begin{cases} \text{Bycatchonly} & \text{if } \frac{MMB}{MMB_{35}} \leq 0.25 \\ \frac{F_{35}(\frac{MMB}{MMB_{35}} - \alpha)}{1 - \alpha} & \text{if } 0.25 < \frac{MMB}{MMB_{35}} < 1 \\ F_{35} & \text{if } MMB > MMB_{35} \end{cases} \quad (1)$$

139 Where MMB is the projected MMB in the current survey year after fishing at the F_{OFL} , $MMB_{35\%}$ is the
 140 equilibrium MMB at the time of mating resulting from fishing at $F_{35\%}$, $F_{35\%}$ is the fishing mortality that
 141 reduces the MMB-per-recruit to 35% of unfished levels under constant recruitment, and α determines the
 142 slope of the descending limb of the harvest control rule (set to 0.1 here as specified by the NPFMC).

143 Results

144 All models produced a positive-definite Hessian and had maximum gradient components less than 0.004,
 145 except “Vary both”, which had a maximum gradient component of 0.01 for one of the recruitment deviations
 146 for males (the rest were < 0.004). The smallest viable smoothing penalties tested were 1 and 10 for natural
 147 mortality and catchability (respectively) when they were the only additional time-varying process in the
 148 assessment. When both processes were allowed to vary, the smoothness penalty for natural mortality had to
 149 be increased to 15 or the model did not converge.

150 Fits to the data

151 Models “Vary M ”, “Vary q ”, and “Vary both” all fit the survey MMB better than the status quo model (Fig-
 152 ure 3 and Table 1), particularly in recent years (Figure 4). The status quo model missed the input confidence
 153 intervals of 5 of the last 6 years of survey MMB, but additional estimated time-variation improved these fits.
 154 Fits to the catch data, growth data, and all size-composition data sources can be seen in the supplemen-
 155 tary materials. In general, the fits were similar across models, except for the survey size-composition data,

156 in which there are several years in which models that allowed for additional time-variation produce much
157 better fits than models that did not. Retrospective patterns in the status quo model (Mohn's $\rho = 0.36$)
158 were improved substantially by allowing additional time-variation in either natural mortality or catchability
159 (Figure 5).

160 Estimated population processes and derived quantities

161 Estimated population processes and derived quantities varied among models. The trajectories of the time
162 series of estimated MMB varied strongly among models, and model "Vary both" produced the largest his-
163 torical estimates of MMB (Figure 6). The shapes of the estimated curve representing the probability of
164 undergoing terminal molt for males were similar among models, but the magnitude of the probabilities var-
165 ied, most strongly for males in the 70-90 mm carapace width range (Figure 7). 'Vary both' estimated the
166 highest fraction of sub-industry-preferred size (i.e. <101 mm carapace width) crab undergoing terminal molt.
167 Trajectories of estimated fishing mortality were similar across models, but variability within years existed
168 due to differing estimates of population size (Figure 7). Patterns in estimated recruitment were similar for
169 all models, but the relative magnitudes varied (Figure 7).

170 Estimated natural mortality across models varied widely (Figure 8). Both 'Vary both' and 'Vary M ' esti-
171 mated higher natural mortality in recent years compared to historical estimates, but estimates from 'Vary
172 both' increased sharply starting in 2017 and ended with estimates in 2020 nearly double that of 'Vary M '.
173 Estimates of mean natural mortality were smaller for models in which natural mortality was allowed to vary
174 over time than for those in which natural mortality was constant over time. The shapes of the estimated
175 survey selectivity curves were similar among all models; the largest changes were seen in the catchability
176 coefficient (see supplementary figures). Models in which catchability was time-varying estimated average
177 catchabilities similar to the experimentally implied catchability. However, the variability in estimated catch-
178 ability for these models was large, with estimated values ranging from ~ 0.2 to ~ 1 (Figure 8).

179 Differences in estimated population processes and fits to the data resulted in large differences in management
180 advice (Table 2). The terminal year of estimated MMB varied from 43,290 t to 133,510 t, with models
181 estimating time-varying M returning much lower MMB than those that did not. The corresponding target
182 biomasses ($B_{35\%}$) were also much lower for models incorporating time-varying M because the projections
183 used to calculate $B_{35\%}$ are based on the terminal years of estimated M , which were quite high (Figure 8). An
184 additional effect of increases in estimated M (and changes in the probability of terminally molting; Figure 7)
185 were large increases in $F_{35\%}$ (Table 2). In spite of large differences in the estimated MMB, the management
186 advice from 'Vary q ' was only 10% more than 'Vary M ' (77.08 vs. 70.88 kt). This similarity in OFLs is a
187 function of the large $F_{35\%}$ and small $B_{35\%}$ from 'Vary M ' relative to 'Vary q '. However, if both processes
188 were allowed to vary in the assessment ('Vary both'), the calculated OFL was 81% smaller than the when
189 only one process was allowed to vary. Furthermore, if the smoothness penalty used for 'Vary both' was used
190 in 'Vary M ', the calculated OFLs were similar, suggesting relatively unstable estimation of time-varying M .

191 Discussion

192 Time-variation in M and/or q appears to be an issue for snow crab, but data to inform changes in population
193 processes over time are lacking. Allowing M or q to vary over time within the assessment lead to improved
194 fits to the data and reductions in retrospective patterns, but the management advice differed by almost
195 an order of magnitude depending on what processes were allowed to vary and how the processes were
196 constrained within the estimation process. Further, estimates of time-varying natural mortality among
197 assessment variants and other published models fit to the same data (Murphy et al., 2018) were quite
198 different in character (Figure 8). Ultimately, the Crab Plan Team, which is the first level of peer review
199 for the assessments used for crab in the eastern Bering Sea, chose not to endorse models that allowed time-
200 varying q or M for use in management because the estimates of q and M varied more drastically than seemed
201 reasonable and there was no clear mechanism to support the variability.

202 Improvements in fit and reductions in retrospective patterns with additional model flexibility is an expected
203 outcome and is not unique to either snow crab or size-structured models. Szuwalski et al. (2019) demonstrated
204 a similar outcome in a simulation study based on a cod-like life history with age-structured assessment
205 models. Retrospective patterns were induced by simulating data with time-variation in growth, selectivity,
206 or natural mortality and fitting assessment models that did not model time-variation in those processes.
207 Next, assessment models that allowed either growth, selectivity, or natural mortality to vary over time were
208 fit to the data. Implementing any of these time-varying processes reduced the magnitude of retrospective
209 patterns, but management advice resulted in over- or under-exploiting the stock if the incorrect process
210 was allowed to vary. One of the main recommendations of the paper was that an understanding of what
211 process is time-varying is recommended before implementation of time-variation in integrated assessments.
212 The lack of a mechanistic understanding for changes in snow crab was the primary reason the models with
213 time-variation in M and/or q were not used in management.

214 Much effort has been expended exploring methods to estimate time-variation in natural mortality and se-
215 lectivity in recent years (e.g., Miller and Hyun, 2017; Jiao et al. 2012; Jacobsen et al. 2019). The CAPAM
216 special issue on selectivity (Maunder et al., 2014) presented papers on methodology for using random-effects
217 to estimate time-variation in selectivity (Nielsen and Berg, 2014) and best practices in modeling time-varying
218 selectivity (Martell and Stewart, 2014). Simulation studies have been used to suggest that estimating M
219 at a minimum should be the default in stock assessment (Johnson et al., 2014). More recently, Aldrin et
220 al. (2021) suggested that accounting for variability across time using simple models improves performance
221 over time-invariant M .

222 In spite of the effort spent estimating time-varying catchability, selectivity, and natural mortality individually,
223 less effort has been spent understanding the feasibility of estimating time-variation in multiple confounded
224 processes within a stock assessment. This is perhaps because the confounding of processes like natural
225 mortality and catchability is recognized as a central challenge in assessment even without considering time-
226 variation (Maunder and Piner, 2014). It has also been shown to be difficult to estimate time variation in
227 a single population process with the data often available for population dynamics modeling, much less two
228 (Johnson et al., 2014, Lee et al., 2011). However, moving forward, the need to estimate time-variation in
229 multiple processes will likely be an increasingly prevalent problem as populations respond to a changing
230 environment (Szuwalski and Hollowed, 2016). Changes in distribution (Pinksy et al., 2013), recruitment
231 (Szuwalski et al., 2015), growth (Audzijonyte et al., 2020), and natural mortality (Audzijonyte et al., 2016)
232 are already being observed in harvested marine populations. If appropriate ways of incorporating multiple
233 processes varying over time into assessment cannot be found, the knock-on effects of retrospective patterns
234 and erroneous management advice will become increasingly common. This may result in an eroded potency
235 of previously effective management (Hilborn et al., 2021).

236 Given the outcomes of this analysis, it is not clear if the estimation of time-variation in confounded processes
237 is a problem we can model our way out of with the currently available data for snow crab. Completing these
238 sorts of analyses with a wider range of life histories, population processes considered (e.g. growth), and data
239 availabilities (both real world and simulated) could be useful to better understand the potential for estimating
240 time-variation in confounded processes in stock assessment. Identifying methods for specifying smoothness
241 parameters would be useful for practical implementation of time-varying processes in stock assessment given
242 their impact on the analysis presented here. More longitudinal data are likely needed to directly inform
243 the estimation of time-variation in confounded processes, but the continuous tagging, laboratory, and net
244 efficiency studies that would be needed to provide these data will be expensive. So, cost-benefit analyses
245 aimed at understanding the value of information derived from the needed studies to estimate time-variation
246 in confounded processes should also be performed. These analyses could include management strategy
247 evaluations aimed at understanding the improvement in management outcomes coming from assessments
248 that can estimate time-variation in confounded processes and simpler strategies that do not attempt to do
249 so.

250 **Acknowledgments**

251 I'd like to thank Jack Turnock for passing the status quo code down to me upon his retirement. I also thank
252 Kelli Johnson and Shareef Siddeek for comments that improved this manuscript.

253 **Supplementary materials**

254 The github repository including the code used to perform the analysis and additional figures describing the
255 fit of the models to the data can be found at: https://github.com/szuwalski/snow_confounded.

References

- 256 Aldrin, M., Aanes, F.L., Tvette, I.F., Aanes, S., Subbey, S. 2021. Caveats with estimating natural mortality rates in stock assessment models using age-aggregated catch data and abundance indices. *Fish. Res.* doi.org/10.1016/j.fishres.2021.106071
- 257 Audzijonyte, A., Richards, S.A., Stuart-Smith, R.D., Pecl, G., Edgar, G.J., Barrett, N.S., Payne, N., Blanchard, J.L. 2020. Fish body sizes change with temperature but not all species shrink with warming. *Nat. Eco. Evo.* 4(6): 809-814.
- 260 Audzijonyte, A., Fulton, E., Haddon, M., Helidoniotis, F., Hobday, A.J., Kuparinen, A., Morrongiello, J., Smith, A.D.M., Upston, J., Waples, R. 2016. Trends and management implications of human-influenced life-history changes in marine ectotherms. *Fish Fish.* 17(4): 1005-1028.
- 263 Clark, W.G. 1991. Groundfish exploitation rates based on life history parameters. *Can. J. Fish. Aquat. Sci.* 48: 734-750.
- 266 Fournier, D.A. and C.P. Archibald. 1982. A general theory for analyzing catch-at-age data. *Can. J. Fish. Aquat. Sci.* 39:1195-1207.
- 268 Fournier, D.A., H.J. Skaug, J. Ancheta, J. Ianneli, A. Magnusson, M.N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.* 27:233-249.
- 270 Hilborn, R. et al. 2021. Effective fisheries management instrumental in improving fish stock status. *Proc. Natl. Acad. Sci.* 117(4): 2218-2224.
- 273 Jacobsen, N.S., Essington, T.E. 2018. Natural mortality augments population fluctuations of forage fish. *Fish Fish.* 19(5): 791-797.
- 275 Jacobsen, N.S., Thorson, J.T., Essington, T.E. 2019. Detecting mortality variation to enhance forage fish population assessments. *ICES J. Mar. Sci.* 76(10): 124-135.
- 277 Jiao, Y. Smith. E.P. O'Reilly, R., Orth, D.J. 2012. Modelling non-stationary natural mortality in catch-at-age models. *ICES J. Mar. Sci.* 69(1): 105-118.
- 280 Johnson, K.F. et al. 2014. Time-varying natural mortality in fisheries stock assessment models: identifying a default approach. *ICES J. Mar. Sci.* 72(1): 137-150.
- 281 Lee, H.H., Maunder, M.N., Piner, K.R., Methot, R.D. 2011. Estimating natural mortality within a fisheries stock assessment model: An evaluation using simulation analysis based on twelve stock assessment. *Fish. Res.* 109(1): 89-94.
- 283 Martell, S., Stewart, I. 2014. Towards defining good practices for modeling time-varying selectivity. *Fish. Res.* 158 84-95.
- 286 Maunder, M.N. Piner, K.R. 2014. Contemporary fisheries stock assessment :many issues still remain. *ICES J. Mar. Sci.* 71(10): 7-18.
- 288 Maunder, M.N., Crone, P.R., Valero, J.L., Semmens, B.X. 2014. Selectivity: Theory, estimation, and application in fishery stock assessment models. *Fish. Res.* 158: 1-4.
- 290 Methot, R.D. 1990. Synthesis model: An adaptable framework for analysis of diverse stock assessment data. *Int. N. Pac. Fish. Comm. Bull.* 50:259-277.
- 292 Miller, T.J. and Hyun, S.Y. 2017. Evaluating evidence for alternative natural mortality and process error assumptions using a state-space, age-structured assessment model. *Can. J. Fish. Aquat. Sci.* 75(5): 691-703.
- 294 Mohn R. 1999. The retrospective problem in sequential population analysis: an investigation using cod fishery and simulated data, *ICES J. Mar. Sci.* 56: 473-488.
- 296 Murphy, J.T., Rugolo, L.J., Turnock, B.J. 2018. Estimation of annual, time-varying natural mortality and survival for Eastern Bering Sea snow crab with state-space population models. *Fish. Res.* 205: 122-131.
- 298
- 299

- 300 Nielsen, A., Berg, C.W. 2014. Estimation of time-varying selectivity in stock assessments using state-space
301 models. *Fish. Res.* 158: 96-101.
- 302 NOAA, Report of the retrospective working group. Northeast Fisheries Science Center Reference Documents,
303 09-01, 2009. Woods Hole, MA. National Oceanic and Atmospheric Administration [http://www.nefsc.noaa.](http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0901/crd0901.pdf)
304 [gov/nefsc/publications/crd/crd0901/crd0901.pdf](http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0901/crd0901.pdf)
- 305 NPFMC (North Pacific Fishery Management Council). 2007. Environmental Assessment for Amendment
306 24. Overfishing definitions for Bering Sea and Aleutian Islands King and Tanner crab stocks. North Pacific
307 Fishery Management Council, Anchorage, AK, USA..
- 308 Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L. Levin, S.A. 2013. Marine taxa track local climate
309 velocities. *Science.* 341(6151): 1239-1242.
- 310 Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of com-
311 mercial marine fisheries. *Bull. Int. Am. Trop. Tuna. Com.* 1(2): 27-56.
- 312 Shibata, Y. Nagao, J. Narimatsu, Y. Eisuke, M., Suzuki, Y., Tokioka, S., Yamada, M., Kakehi, S., Okamura,
313 H. 2021. Estimating the maximum sustainable yield of snow crab off Tohoku, Japan via a state-space stock
314 assessment model with time-varying natural mortality. *Pop. Ecol.* 63: 41-60.
- 315 Somerton, D.A. Weinberg, K.L., Goodman, S.E. 2013. Catchability of snow crab by the eastern Bering
316 Sea bottom trawl survey estimated using a catch comparison experiment. *Can. J. Fish. Aquat. Sci.* 70:
317 1699-1708.
- 318 Stawitz, C.C., Haltuch, M.A., Johnson, K.F. 2019. How does growth mis-specification affect management
319 advice derived from an integrated fisheries stock assessment model? *Fish. Res.* 213: 12-21.
- 320 Szuwalski, C.S., Vert-Pre, K.A., Punt, A.E., Branch, T.A., Hilborn, R. 2015. Examining common assump-
321 tions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish Fish.*
322 16(4): 633-648.
- 323 Szuwalski, C.S. and Hollowed, A.B. 2016. Climate change and non-stationary population processes in fisheries
324 management. *ICES J. Mar. Sci.* 73(5): 1297-1305.
- 325 Szuwalski, C.S., Ianelli, J.N., Punt, A.E. 2019. Reducing retrospective patterns in stock assessment and
326 impacts on management performance. *ICES J. Mar. Sci.* 75(2): 596-609.
- 327 Szuwalski, C.S., Cheng, W., Foy, R., Hermann, A.J., Hollowed, A.B., Holsman, K., Lee, J., Stockhausen,
328 W., Zheng, J. 2020. Climate change and the future productivity and distribution of crab in the eastern
329 Bering Sea. *ICES J. Mar. Sci.* 78(2): 502-515.
- 330 Taylor, I.G., Methot, R.D. 2013. Hiding or dead? A computationally efficient model of selective fisheries
331 mortality. *Fish. Res.* 142: 75-85.
- 332 Then, A.Y., Hoenig, J.M., Hall, G.H., Hewitt, D.A. 2015. Evaluating the predictive performance of empirical
333 estimators of natural mortality rate using information on over 200 fish species. *ICES J. Mar. Sci.* 72(1):
334 82-92.
- 335 Thompsen, G.G. 1994. Confounding of gear selectivity and natural mortality rate in cases where the former
336 is a nonmonotone function of age. *Can. J. Fish. Aquat. Sci.* 51(12): 2654-2664.
- 337 Thorson, J.T., Monnahan, C.C., Cope, J.M. 2015. The potential impact of time-variation in vital rates on
338 fisheries management targets for marine fishes. *Fish. Res.* 169: 8-17.
- 339 Turnock, B.J., 2015. Stock assessment of Eastern Bering Sea snow crab. Stock Assessment and Fishery
340 Evaluation Report for the King and Tanner Crab Fisheries of the Bering Sea and Aleutian Islands Regions.
341 2016 Crab SAFE. North Pacific Fishery Management Council, Anchorage, AK, pp. 167-250.
- 342 Wilberg, M.J., Thorson, J.T., Linton, B.C., Berkson, J. 2009. Incorporating time-varying catchability into
343 population dynamics stock assessment models. *Rev. Fish. Sci.* 18(1): 7-24.

344 Appendix A: Population dynamics model description

345 Numbers of sex s of shell condition v and maturity state m at width w in the initial year of the assessment,
 346 $N_{s,v,m,y=1,w}$, were calculated from an estimated vector of numbers at width w by sex s and maturity state
 347 m for males, $\lambda_{s,m,l}$ and numbers at width w by sex s and shell condition v for females (i.e. 2 vectors for each
 348 sex were estimated). Estimated vectors of initial numbers at size by maturity for females were calculated
 349 by splitting the estimated vectors at size by the observed proportion mature in the first year of the survey.
 350 Shell condition is differentiated in the input data for the assessment, but is aggregated over when likelihoods
 351 are calculated, so the brief description in the main text does not include shell condition.

$$N_{s,v,m,y=1,w} = \begin{cases} \Omega_{s,w}^{obs} \lambda_{s,1,w} & \text{if } v = \text{new}; m = \text{mat}, s = \text{fem} \\ 1 - \Omega_{s,w}^{obs} \lambda_{s,1,w} & \text{if } v = \text{new}; m = \text{imat}, s = \text{fem} \\ \lambda_{s,2,w} & \text{if } v = \text{old}; m = \text{mat}, s = \text{fem} \\ 0 & \text{if } v = \text{old}; m = \text{imat} \end{cases} \quad (2)$$

352 Initial numbers at size for males were all assumed to be new shell.

$$N_{s,v,m,y=1,w} = \begin{cases} \lambda_{s,1,w} & \text{if } v = \text{new}; m = \text{mat}, s = \text{male} \\ \lambda_{s,2,w} & \text{if } v = \text{new}; m = \text{imat}, s = \text{male} \\ 0 & \text{if } v = \text{old}; m = \text{mat}, s = \text{male} \\ 0 & \text{if } v = \text{old}; m = \text{imat}, s = \text{male} \end{cases} \quad (3)$$

353 The dynamics after the initial year were described by:

$$N_{s,v,m,y+1,w} = \begin{cases} \Omega_{s,w} \kappa_{s,w'} Q_{s,imat,y,w'} X_{s,w',w} & \text{if } v = \text{new}; m = \text{mat} \\ 1 - \Omega_{s,w} \kappa_{s,w'} Q_{s,imat,y,w'} X_{s,w',w} + Rec_y^\epsilon Pr_w & \text{if } v = \text{new}; m = \text{imat} \\ Q_{s,mat,y,w'} & \text{if } v = \text{old}; m = \text{mat} \\ (1 - \kappa_{s,w'}) Q_{s,imat,y,w'} & \text{if } v = \text{old}; m = \text{imat} \end{cases} \quad (4)$$

354 Where $\Omega_{s,w}$ was the probability of having undergone terminal molt at width w for sex s (a freely estimated
 355 vector for both males and females constrained by penalties on smoothness), $\kappa_{s,w'}$ was the probability of
 356 molting for an immature crab of sex s at width w (set to 1 for all immature crab and zero for all mature
 357 crab), and $X_{s,w,w'}$ was the size transition matrix describing the probability of transitioning from size w' to
 358 size w for sex s . $Q_{s,m,y,w'}$ was the number of crab of sex s , maturity state m , and width w surviving natural
 359 and fishing mortality during year y :

$$Q_{s,m,y,w} = \sum_v N_{s,v,m,y,w} e^{Z_{s,v,m,y,w}} \quad (5)$$

360 Where $N_{s,v,m,y,w}$ represented the numbers, N , of sex s during year y of shell condition v and maturity state m
 361 at width w . $Z_{s,v,m,y,w}$ represented the total mortality experienced by the population and consisted of the sum
 362 of instantaneous rates of natural mortality by sex and maturity state, $M_{s,m}$, and fishing mortality, $F_{s,f,y,w}$
 363 from each fishery. Each fishing mortality was subject to selectivity by width w , which varied between sexes
 364 s and fisheries f (and by year y if specified). $M_{s,m}$ was specified in the model based on a maximum assumed

365 age of 20 and Then et al.'s (2015) empirical study on relationships between life history characteristics and
 366 natural mortality. A multiplier $\gamma_{natM,m}$ was estimated subject to constraints (this formulation effectively
 367 specified a mean and standard deviation for a prior distribution for M).

$$Z_{s,v,m,y,w} = \gamma_{natM,m} M_{s,m} + \sum_f S_{s,f,y,w} F_{s,f,y,w} \quad (6)$$

368 Selectivities in the directed and bycatch fisheries were estimated logistic functions of size. Different selec-
 369 tivity parameters were estimated for females and males in the directed fisheries ($S_{fem,dir,w}$ and $S_{male,dir,w}$,
 370 respectively), a single selectivity for both sexes was estimated for bycatch in the groundfish trawl fishery
 371 ($S_{trawl,w}$), and a retention selectivity was estimated for the directed fishery for males ($R_{dir,w}$; all females
 372 were discarded).

$$S_{male,dir,w} = \frac{1}{1 + e^{-S_{slope,m,d}(W_w - S_{50,m,d})}} \quad (7)$$

$$S_{fem,dir,w} = \frac{1}{1 + e^{-S_{slope,f,d}(W_w - S_{50,f,d})}} \quad (8)$$

$$S_{trawl,w} = \frac{1}{1 + e^{-S_{slope,t}(W_w - S_{50,t})}} \quad (9)$$

$$R_{dir,w} = \frac{1}{1 + e^{-S_{slope,m,d}(W_w - S_{50,m,d})}} \quad (10)$$

373 Where $S_{slope,s,f}$ was the slope of the logistic curve for sex s in fishery f and $S_{50,s,f}$ was the width at 50%
 374 selection for sex s in fishery f . Catches for all fisheries were modeled as pulse fisheries in which all catch was
 375 removed instantaneously (i.e. no natural mortality occurred during the fishery). Catch in fishery f during
 376 year y was calculated as the fraction of the total fishing mortality, $F_{s,f,y,w}$, applied to a given sex s in a
 377 fishery f times the biomass removed by all fisheries for that sex.

$$C_{male,dir,y} = \sum_w \sum_v \sum_m w_{male,w} \frac{R_w F_{male,dir,y,w}}{F_{male,dir,y,w} + F_{trawl,y,w}} N_{male,v,m,y,w} e^{-\delta_y M_{s,m}} (1 - e^{-(F_{male,dir,y,w} + F_{trawl,y,w})}) \quad (11)$$

$$C_{male,tot,y} = \sum_w \sum_v \sum_m w_{male,w} \frac{F_{male,dir,y,w}}{F_{male,dir,y,w} + F_{trawl,y,w}} N_{male,v,m,y,w} e^{-\delta_y M_{s,m}} (1 - e^{-(F_{male,dir,y,w} + F_{trawl,y,w})}) \quad (12)$$

$$C_{fem,dir,y} = \sum_w \sum_v \sum_m w_{fem,w} \frac{F_{fem,dir,y,w}}{F_{fem,dir,y,w} + F_{trawl,y,w}} N_{fem,v,m,y,w} e^{-\delta_y M_{s,m}} (1 - e^{-(F_{fem,dir,y,w} + F_{trawl,y,w})}) \quad (13)$$

$$C_{m+f,trawl,y} = \sum_s \sum_w \sum_v \sum_m w_{s,w} N_{s,v,m,y,w} e^{-\delta_y M_{s,m}} (1 - e^{-F_{trawl,y,w}}) \quad (14)$$

378 Where δ_y was the mid point of the fishery (all fisheries were assumed to occur concurrently and the midpoint
 379 was based on the directed fishery, which accounts for the vast majority of the fishing mortality) and $w_{s,w}$
 380 was the weight at width w for sex s . Trawl data and discard data were entered into the model with an
 381 assumed mortality of 80% and 30%, respectively. Fully-selected fishing mortality parameters for fishery f
 382 were estimated as a logged average over a given time period (F_{avg}^{log}) with yearly deviations around that mean
 383 ($F_{dev,y}^{log}$).

$$F_{f,y} = e^{(F_{avg,f}^{log} + F_{dev,f,y}^{log})} \quad (15)$$

384 Selectivity for the survey was estimated for 2 eras in the base model: 1982-1988 and 1989-present. Selectivity
 385 was assumed to be logistic and separate parameters representing the carapace width at which selection
 386 probability equal 50% and 95% ($s_{50,s,e}$ and $s_{95,s,e}$, respectively) were estimated for males and females in the
 387 second era (1989-present). Separate catchability coefficients ($q_{s,e}$) were estimated for males and females in
 388 all eras.

$$S_{surv,s,w,e} = \frac{q_{s,e}}{1 + e^{-\log(19) \frac{W_w - s_{50,s,e}}{s_{95,s,e} - s_{50,s,e}}}} \quad (16)$$

389 Survey selectivity was informed by experimental surveys during the years 2009 and 2010. A portion of the
 390 NMFS summer survey tows were accompanied by an industry vessel using nephrops trawls with an assumed
 391 selectivity of 1 for all size classes. To represent the proportion of the population covered by the experiment,
 392 a vector was freely estimated for males, S_y^{free} (subject to a scaling parameter), and a logistic curve was
 393 estimated for females.

$$S_{ind,s,w,y} = \begin{cases} \frac{q_{ind,s,y}}{1 + e^{-\log(19) \frac{L_l - s_{50,s,y}}{s_{95,s,y} - s_{50,s,y}}}} & \text{if } s = \text{female} \\ q_{ind,s,y} S_y^{free} & \text{if } s = \text{male} \end{cases} \quad (17)$$

394 Based on this logic, after identifying the fraction of the crab at length covered by the experimental surveys, the
 395 size composition of the NMFS data collected simultaneously with the experimental trawls can be calculated
 396 by multiplying the numbers at carapace width ‘available’ to the experimental trawls by the overall survey
 397 selectivity, $S_{surv,s,w,y}$. The predicted numbers at size for the NMFS and industry data from the selectivity
 398 experiment were calculated by multiplying the respective selectivities by the survey numbers at size

$$S_{nmfs,s,w,y} = S_{ind,s,w,y} S_{surv,s,w,y} \quad (18)$$

399 Mature male and female biomass (MMB and FMB, respectively) were fit to in the objective function and
 400 were the product of mature numbers at length during year y and the weight at size, $w_{s,w}$:

$$MMB_y = \sum_{l,v} w_{male,w} N_{male,v,mat,y,l} \quad (19)$$

$$FMB_y = \sum_{l,v} w_{fem,w} N_{fem,v,mat,y,l} \quad (20)$$

$$w_{s,l} = \alpha_{wt,s} w_w^{\beta_{wt,s}} \quad (21)$$

401 Mature biomass can be calculated for different time through out the year, in which case the numbers at size
 402 are decremented by the estimated natural mortality. Parameters $\alpha_{wt,s}$ and $\beta_{wt,s}$ were estimated outside of
 403 the assessment model and specified in the control file.

404 Molting and growth occur before the survey. Immature crab were assumed to molt every year with an
 405 estimated probability of having undergone terminal molt based on carapace width w (in all the scenarios
 406 presented here, the probability of molting was 1 for all immature animals). For crab that molt, the growth
 407 increment within the size-transition matrix, $X_{s,w,w'}$, was based on a linear relationship between predicted pre-
 408 and post-molt carapace width, ($\hat{W}_{s,w}^{pre}$ and $\hat{W}_{s,w}^{post}$, respectively) and the variability around that relationship
 409 was characterized by a discretized and renormalized gamma function, $Y_{s,w,w'}$.

$$X_{s,w,w'} = \frac{Y_{s,w,w'}}{w' Y_{s,w,w'}} \quad (22)$$

$$Y_{s,w,w'} = (\Delta_{w,w'})^{\frac{L_{s,w} - (\bar{W}_w - 2.5)}{\beta_s}} \quad (23)$$

$$\hat{L}_{s,w}^{post} = \alpha_s + \beta_{s,1} hatW_{s,w}^{pre} \quad (24)$$

$$\Delta_{w,w'} = \bar{L}_{w'} + 2.5 - W_w \quad (25)$$

410 $\hat{W}_{s,l}^{post,1}$ was the predicted post-molt carapace width and $\Delta_{w,w'}$ is the molt increment at size.

411 An average recruitment for the assessment period (1982-present) and yearly deviations around this average
 412 were estimated for both males and females. This modeling assumption was implemented because there
 413 appear to be differences between sexes in recruitment to the model and not allowing for these differences
 414 resulted in large retrospective patterns. Each year's estimated recruitment was allocated to size bins based
 415 on a discretized and renormalized gamma function with parameters specified in the control file.

$$Rec_{y,s} = e^{(Rec_{avg,s} + Rec_{dev,y,s})} \quad (26)$$

416

$$Pr_w = \frac{(\Delta_{1,w})^{\alpha_{rec}/\beta_{rec}} e^{-\Delta_{1,w}/\beta_{rec}}}{w' (\Delta_{1,w'})^{\alpha_{rec}/\beta_{rec}} e^{(-\Delta_{1,w'}/\beta_{rec})}} \quad (27)$$

417 For models in which separate vectors of recruitment deviations were estimated for males and females, a
 418 separate average recruitment was also estimated (in log space). Each vector of deviations was also subject
 419 to a smoothing penalty, but were not linked directly in any way (e.g., priors on the ratio of estimated male
 420 to female average recruitment).

421 Three general types of likelihood components were used to fit to the available data. Multinomial likelihoods
 422 were used for size-composition data, log-normal likelihoods were used for indices of abundance data, and
 423 normal likelihoods were used for catch data, growth data, priors, and penalties. Multinomial likelihoods
 424 were implemented in the form:

$$L_x = \lambda_x \prod_y N_{x,y}^{eff} \prod_l p_{x,y,l}^{obs} \ln(\hat{p}_{x,y,l}/p_{x,y,l}^{obs}) \quad (28)$$

425 L_x was the likelihood associated with data component x , where λ_x represented an optional additional weight-
 426 ing factor for the likelihood, $N_{x,y}^{eff}$ was the effective sample sizes for the likelihood, $p_{x,y,l}^{obs}$ was the observed
 427 proportion in size bin l during year y for data component x , and $\hat{p}_{x,y,l}$ was the predicted proportion in size
 428 bin l during year y for data component x .

429 Log normal likelihoods were implemented in the form:

$$L_x = \lambda_x \prod_y \frac{(\ln(\hat{I}_{x,y}) - \ln(I_{x,y}))^2}{2(\ln(CV_{x,y}^2 + 1))} \quad (29)$$

430 L_x was the contribution to the objective function of data component x , λ_x was any additional weighting
 431 applied to the component, $\hat{I}_{x,y}$ was the predicted value of quantity I from data component x during year y ,
 432 $I_{x,y}$ was the observed value of quantity I from data component x during year y and $CV_{x,y}$ was the coefficient
 433 of variation for data component x during year y .

434 Normal likelihoods were implemented in the form:

$$L_x = \lambda_x \prod_y (\hat{I}_{x,y} - I_{x,y})^2 \quad (30)$$

435 L_x was the contribution to the objective function of data component x , λ_x was represents the weight applied
 436 to the data component (and can be translated to a standard deviation), $\hat{I}_{x,y}$ was the predicted value of

437 quantity I from data component x during year y , $I_{x,y}$ was the observed value of quantity I from data
438 component x during year y .

439 Smoothing penalties were also placed on some estimated vectors of parameters in the form of normal like-
440 lihoods on the second differences of the vector with a user-specified weight. Weightings of all likelihoods
441 and penalties can be found in the .CTL file in the github repository associated with this paper noted in the
442 acknowledgements.

Table 1: Contribution to the objective function by individual likelihood component by modeling scenario.

Likelihood component	Status quo	Vary q	Vary M	Vary both
Recruitment	71.12	70.7	62.97	69.83
deviations				
Initial numbers	2.83	2.86	2.81	2.59
old shell males				
small length bins				
ret fishery length	194.07	189.63	182.27	180.54
total fish length	560.36	554.67	546.02	536.71
(ret + disc)				
female fish length	127.32	128.3	129.98	126.79
survey length	2298.23	2275.79	2208.05	2228.97
trawl length	169.34	164.05	151.31	165.36
2009 BSFRF	-45.58	-45.9	-46.92	-44.82
length				
2009 NMFS study	-36.62	-37	-37.86	-35.78
area length				
M multiplier prior	34.55	40.78	11.44	13.14
maturity smooth	45.6	42.6	29.55	34.71
growth males	0	0	0	0
growth females	0	0	0	0
2009 BSFRF	0.49	0.03	0.09	0.15
biomass				
2009 NMFS study	0.34	0.04	0.06	0.08
area biomass				
cpue q	0.4	0.48	0.19	0.56
retained catch	6.02	3.91	1.21	1.69
discard catch	106.68	116.94	41.42	46.54
trawl catch	11.64	5.62	7.85	5.53
female discard	4	4.67	5.71	7.03
catch				
survey biomass	215.85	126.53	79.96	77.08
F penalty	23.97	21.48	23.83	22.32
2010 BSFRF	5.53	2.93	3.4	1.56
Biomass				
2010 NMFS	6.42	1.85	3.55	4.14
Biomass				
Extra weight	273.98	274.43	267.88	265.7
survey lengths				
first year				
2010 BSFRF	-24.2	-23.6	-22.6	-23.08
length				
2010 NMFS	-30.65	-29.33	-30.84	-31.08
length				
smooth selectivity	1.22	1.3	1.26	1.22
smooth female	0	0	0	0
selectivity				
init nos smooth	32.25	32.84	31.03	31.17
constraint				
Total	4055.16	3926.6	3653.62	3688.65

Table 2: Reported management quantities for each scenario considered. Reported MMB is for the final year, natural mortality (M) is the average over the entire time series for mature males, and average recruitment (avg_rec) is for males.

Model	MMB	B35	F35	FOFL	OFL	M	avg_rec
Status quo	133.51	121.47	1.23	1.23	88.90	0.29	103.91
Vary q	121.61	137.56	1.94	1.94	77.08	0.30	132.86
Vary M	43.29	17.85	6.29	6.29	70.88	0.59	152.61
Vary both	92.20	28.06	12.46	1.86	14.72	0.58	241.96

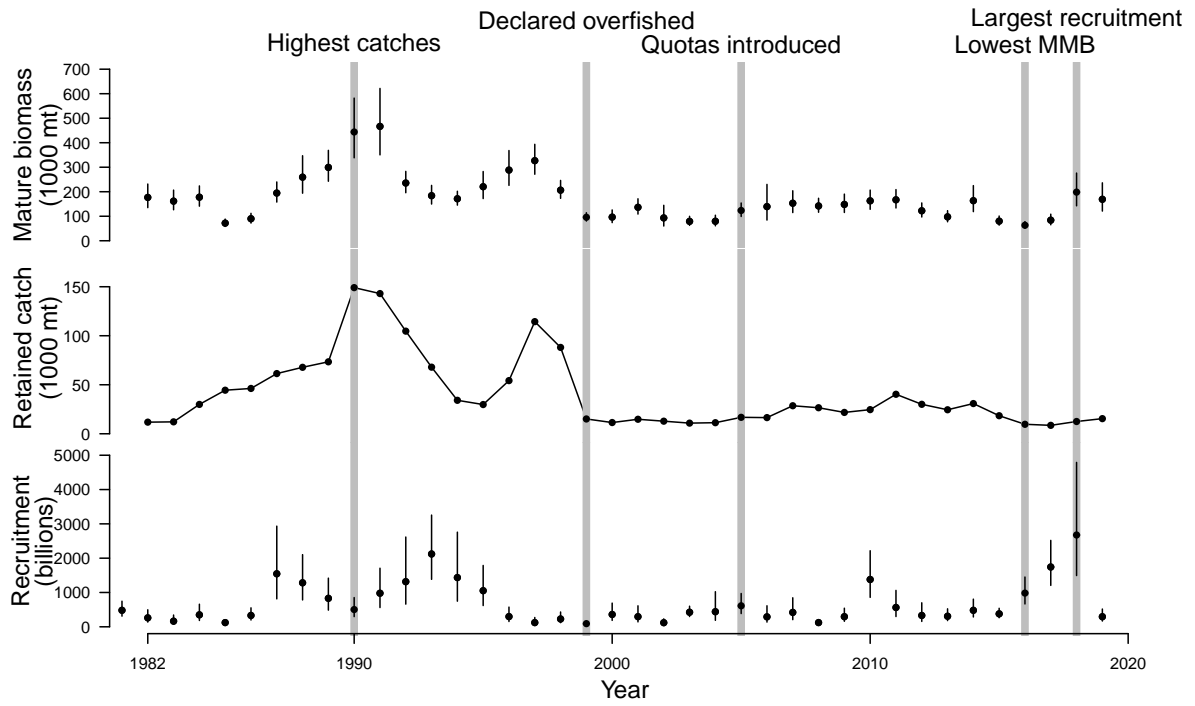


Figure 1: Graphical history of the snow crab fishery in the eastern Bering Sea. Mature biomass are the observed values in the survey, retained catch are reported from fish ticket data, and recruitment is the number of crab sized 40 to 55 mm carapace width observed in the survey.

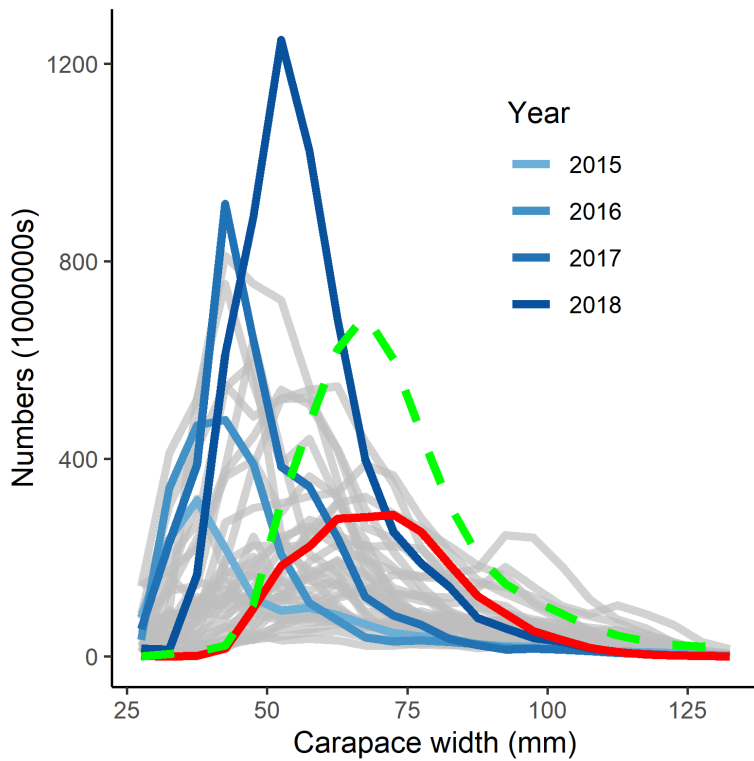
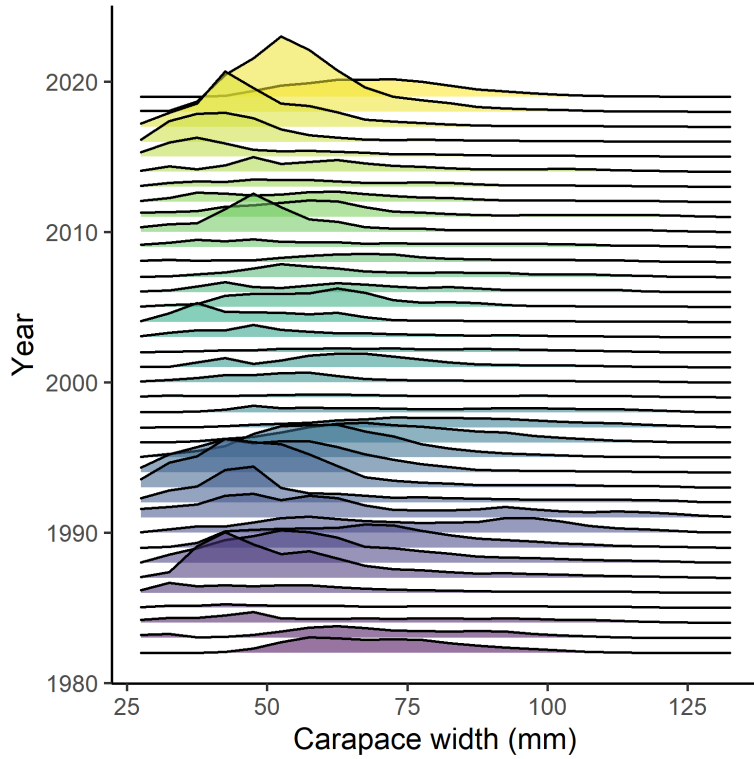


Figure 2: Numbers at length from the survey. Top figure shows the relative numbers at length over time in which the height of the polygon for a given year represents the number of crab observed in that size class. Bottom figure shows the same data, but overlaid. Highlighted years show the recruitment of the 2010 cohort to the survey gear in 2015 and the subsequent reduction of the cohort in 2019 (red line). Dashed green line represents the approximate expected numbers at length given an application of growth, fishery removals, and natural mortality to the numbers at length from 2018.

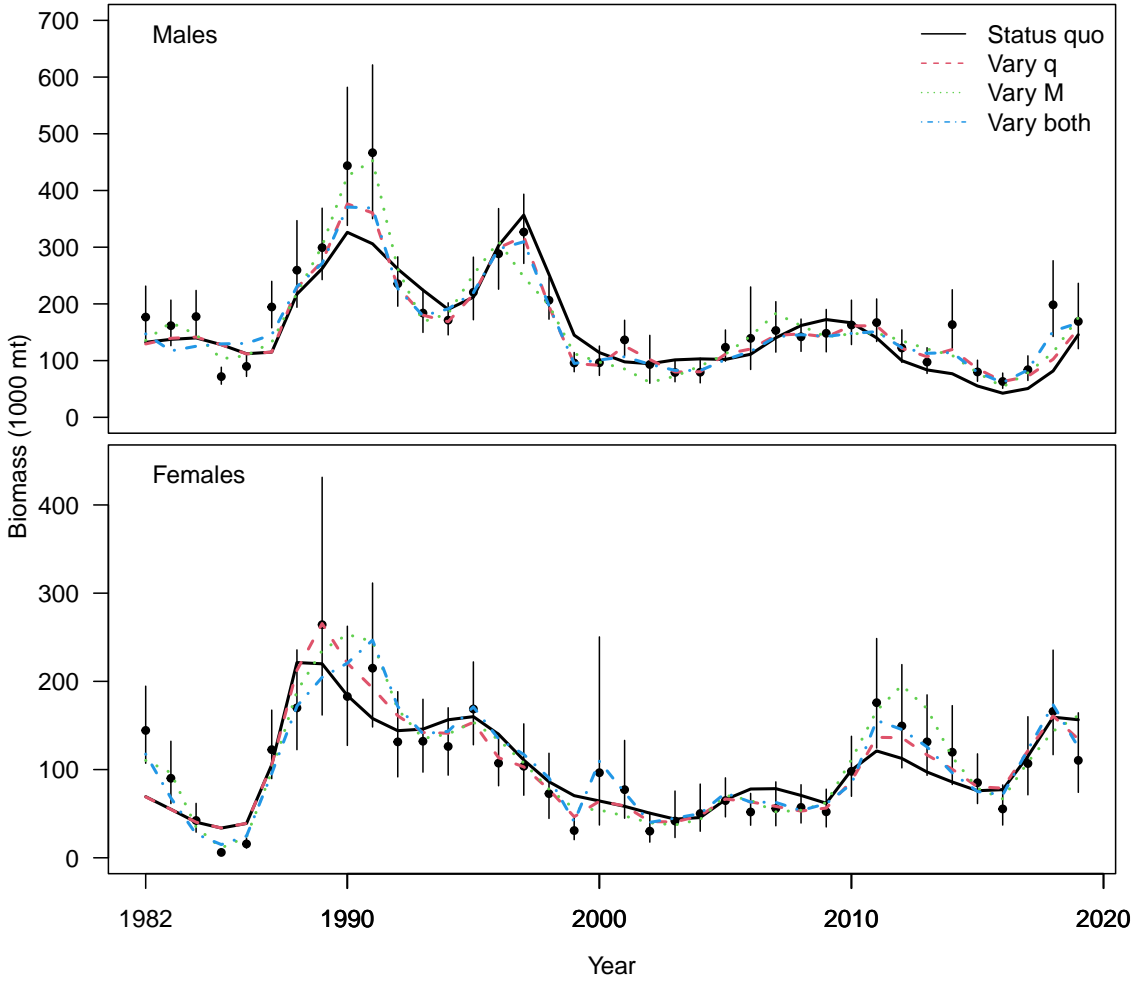


Figure 3: Model fits to the observed mature male biomass at survey with associated confidence intervals.

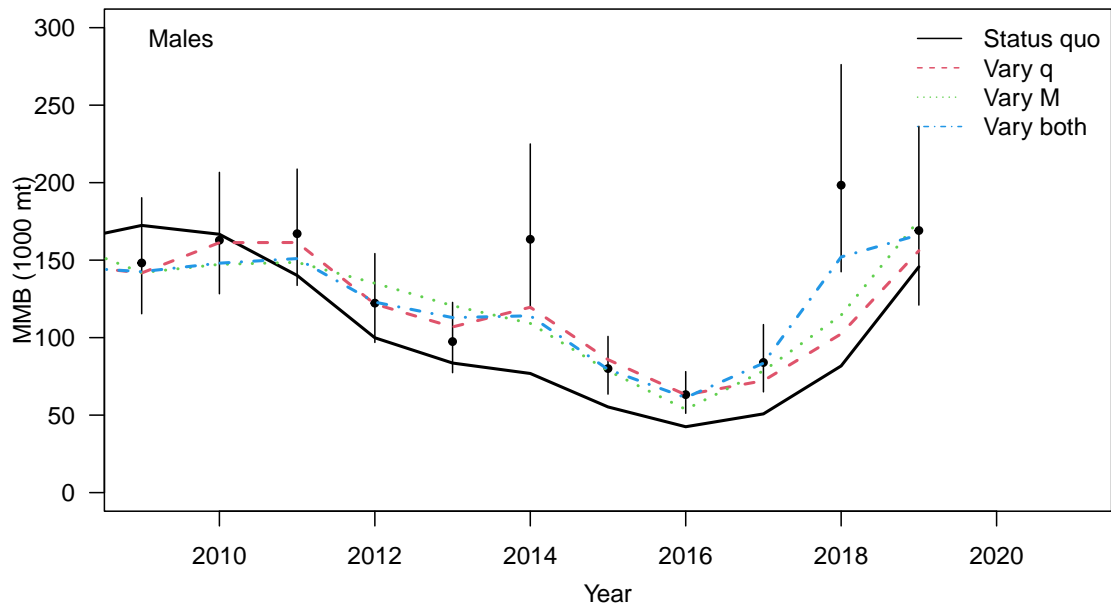


Figure 4: Model fits to the observed mature male biomass at survey 2009-present, note a change in the y-axis from figure 3.

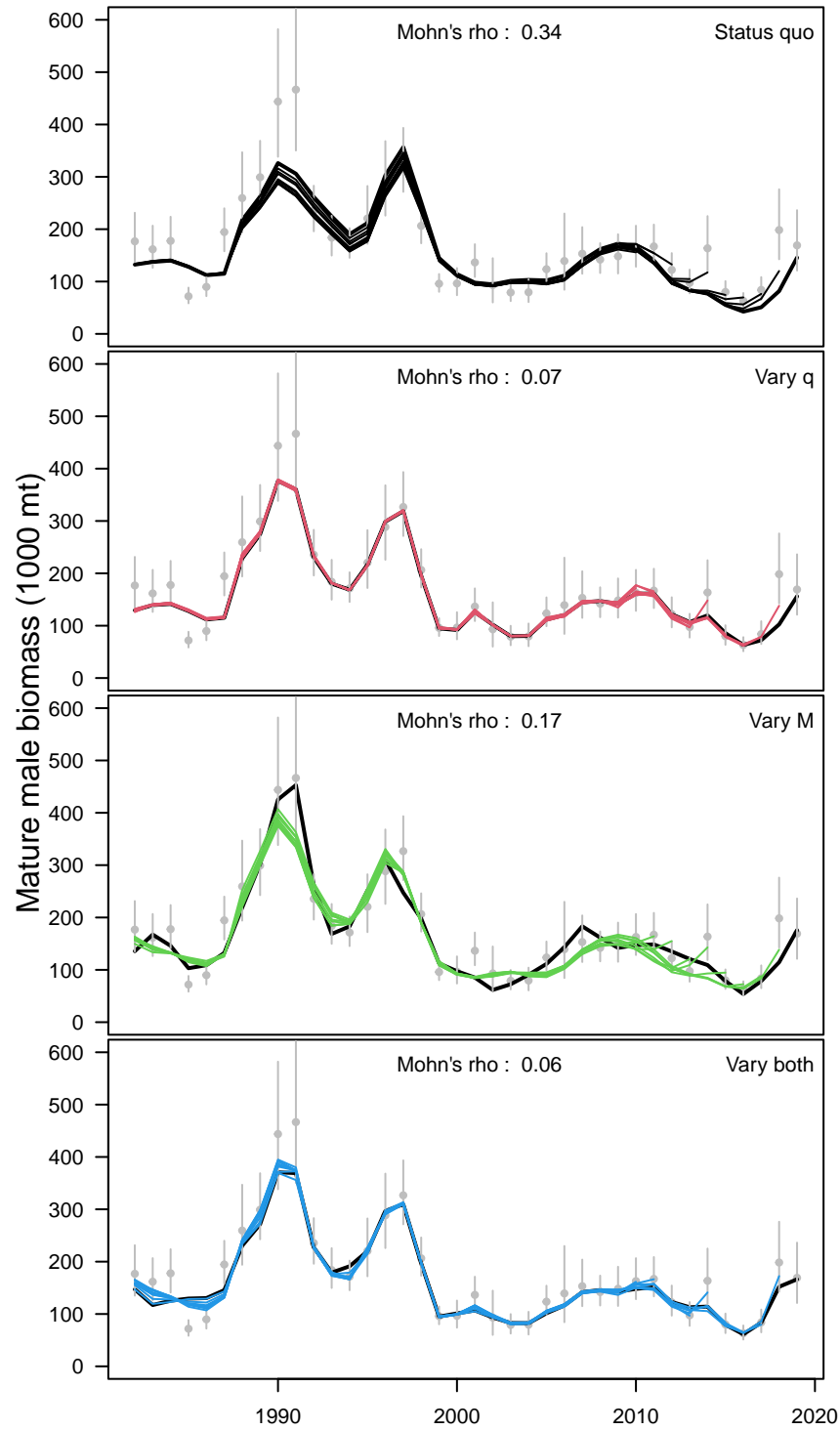


Figure 5: Retrospective patterns in mature male biomass (grey points with confidence intervals) for all models in the analysis. Mohn's rho represents the average deviation of estimated MMB of each peel from the reference peel (black lines).

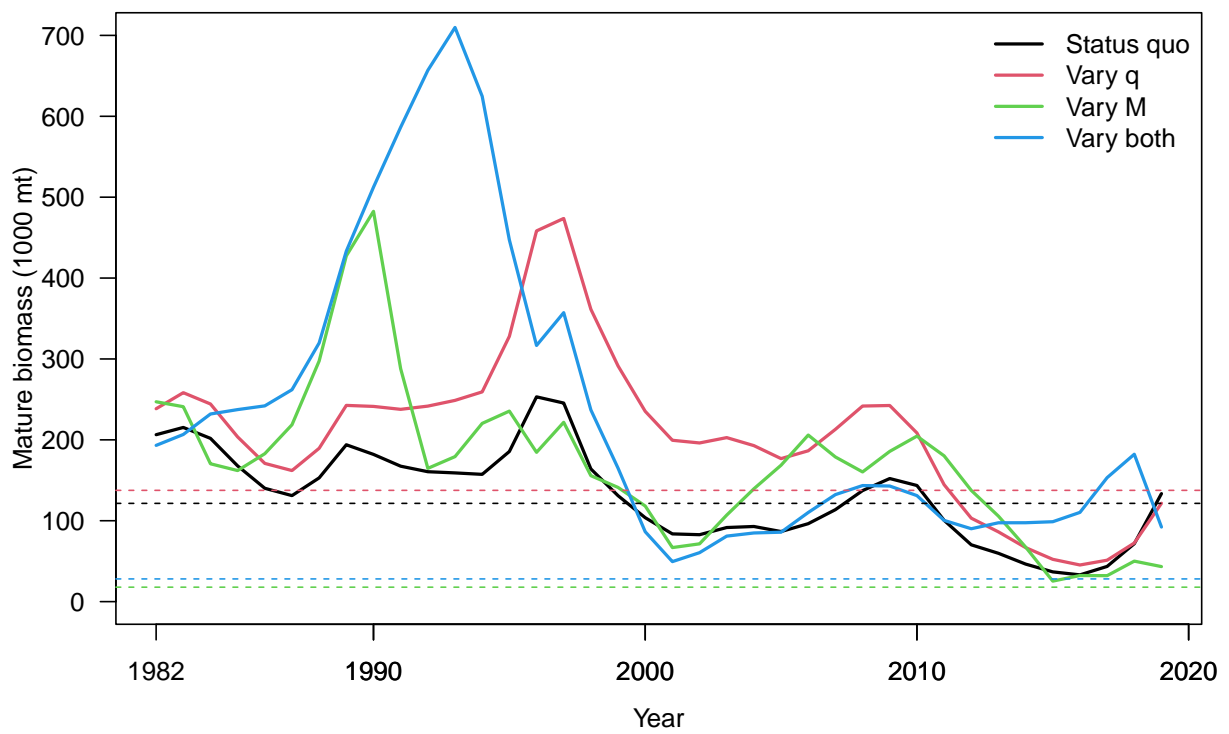


Figure 6: Predicted mature biomass at mating time. Dotted horizontal lines are target biomasses.

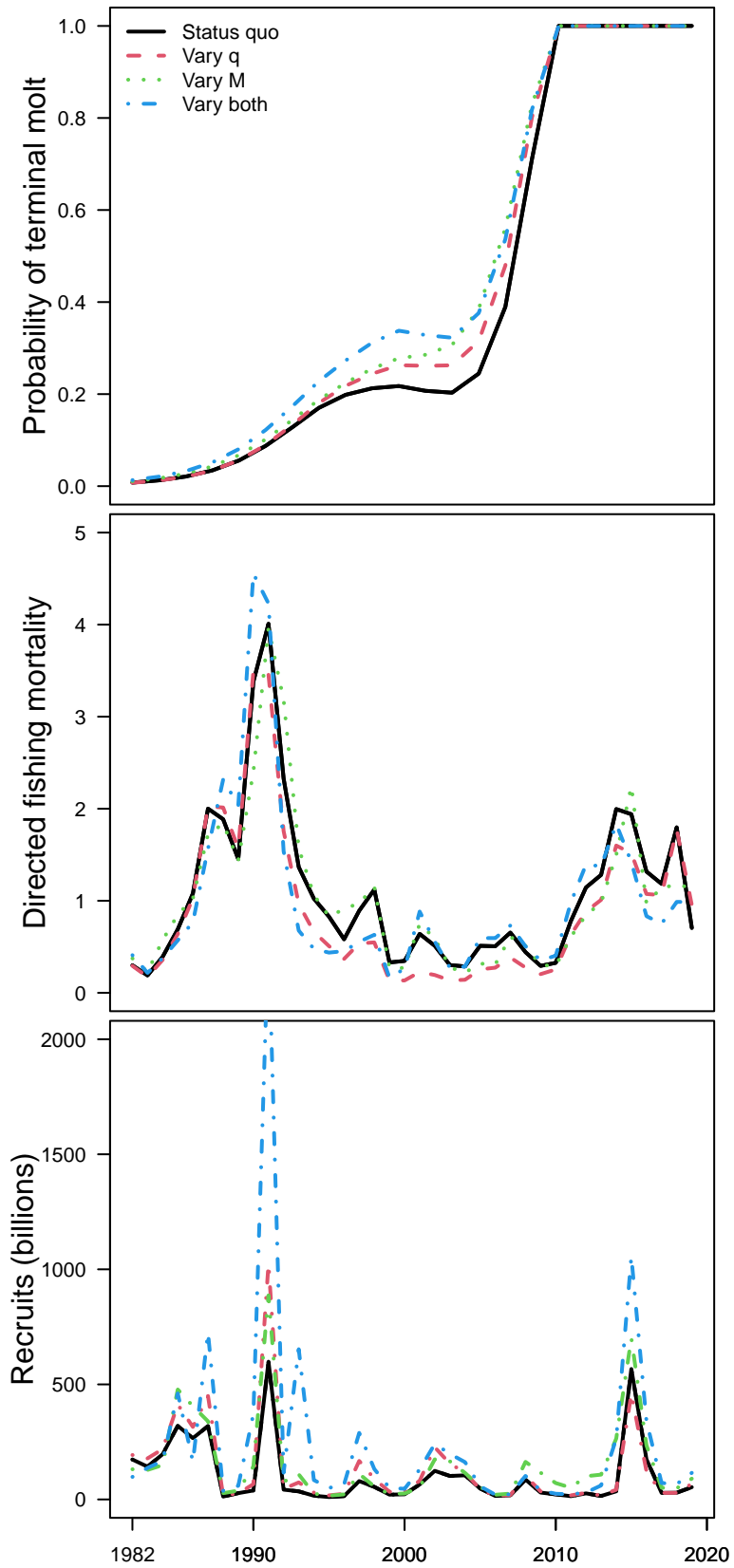


Figure 7: Estimated probability of having undergone terminal molt, directed fishing mortality, and recruitment.

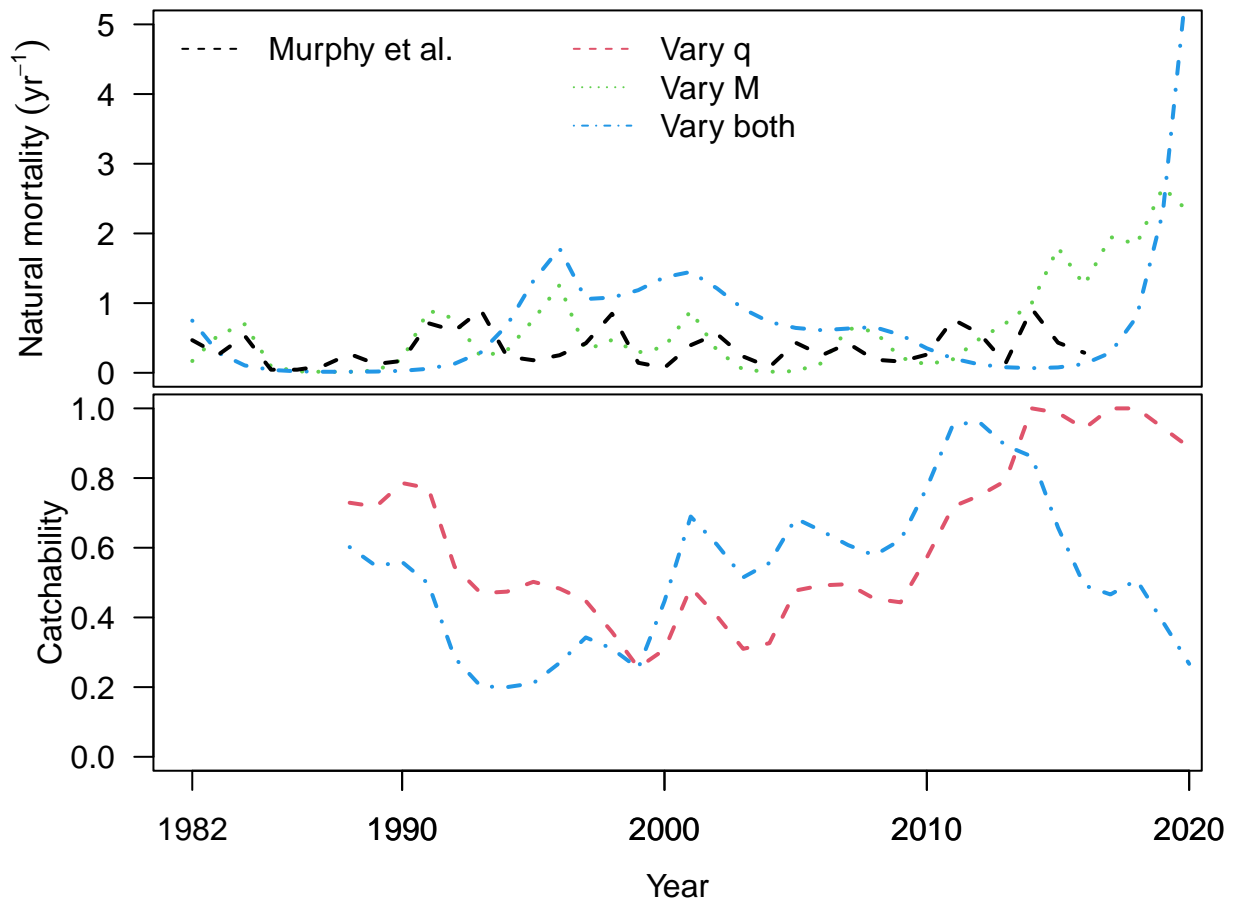


Figure 8: Estimated time-varying natural mortality for mature males and catchability.