

Fish in Space:
Estimating groundfish population distribution in the Gulf of Alaska for management
apportionment by subregion

Kelly Mistry

A thesis
submitted in partial fulfillment of the requirements
for the degree of

Master of Science

University of Washington

2022

Committee:

Mark Scheuerell

Cecilia O'Leary

Sarah Converse

Program Authorized to Offer Degree:
Quantitative Ecology & Resource Management

@Copyright 2022

Kelly Mistry

University of Washington

Abstract

Fish in Space: Estimating groundfish distribution in the Gulf of Alaska for management apportionment by subregion

Kelly Mistry

Chair of the Supervisory Committee:

Mark Scheuerell

School of Aquatic & Fisheries Sciences

Management of fisheries relies on information about biomass of stocks in order to determine how many fish can be sustainably harvested in a given year. In addition to predicting total biomass, it is frequently important to accurately predict the distribution of stock biomass through space in order to avoid local depletions of stock and to more evenly distribute harvest among many stakeholders. Towards that end, this study compares the current modeling approach to predict the geographic apportionment of stock biomass for groundfish in the Gulf of Alaska (GOA), a random walk model, with a delta-GLMM spatiotemporal model implemented using the VAST package in R. These stocks are managed using subregional catch allocation, whereby the GOA is divided into 3 management areas: western, central, and eastern GOA. This analysis uses bottom trawl survey data collected by the Alaska Fisheries Science Center (AFSC) of the National Oceanic Atmospheric Administration National Marine Fisheries Service (NOAA

NMFS) for two species of groundfish, Pacific Ocean Perch (*Sebastes alutus*) and Northern Rockfish (*Sebastes polyspinis*).

Model performance was evaluated using the accuracy of the model estimate from jackknife resampled results for population proportion by subregion compared to survey design-based proportions, and on the precision of the model jackknife estimates. In terms of accuracy, the models performed similarly well, with the mean absolute difference between the model jackknife estimates and the design-based estimates for the random walk results being smaller by 0.086 or less than the delta-GLMM results, with significant overlap in the jackknife absolute difference values. Precision was measured by the CV calculated with the model jackknife results, and the delta-GLMM results had smaller mean CV values by at least 0.105, and very little overlap in the jackknife CV values. However, the precision of the delta-GLMM is small enough that it may lead to significant over- or underestimation compared to the survey design-based proportions and therefore may be a riskier option than the random walk model for estimating subregional catch apportionment for these stocks in the GOA.

33 **Introduction**

34 Fisheries management is a complex process regulating how much of a stock commercial, recreational,
35 and subsistence fishers can harvest. Management strategies take many forms, but the basic goals
36 of most modern fisheries management are to preserve healthy and self-sustaining fish populations,
37 while simultaneously maximizing harvest for the benefit of the fishers and consumers (Costello et al.
38 2016). These goals can be difficult to balance, particularly when fish population characteristics are
39 unknown, and in the past this has led to overfishing and endangering the health of some fish stocks.

40 To determine what a healthy and self-sustaining population for a given stock is, fisheries scientists
41 use statistical modeling to estimate current and past stock biomasses, and project future stock
42 biomasses. There are many statistical models that are used to both meet the needs of management
43 and represent the stock biology and population dynamics as accurately and precisely as possible
44 (Methot 2009). Some examples include abundance-focused models such as age- or size-structured
45 models, or spatial distribution models, which predict where species will occur geographically (Levin
46 and Goodyear 1980, Schnute 1987, Ciannelli et al. 2008). Fisheries scientists are continually looking
47 for ways to improve our statistical models to provide more accurate and precise estimates of biomass
48 for use in management decisions. More accurate and precise estimates on the status of the fish
49 stocks will lead to more confident decision-making to fulfill both management goals of preserving
50 self-sustaining populations and maximizing harvest.

51 This study focuses on the Gulf of Alaska (GOA) groundfish fishery, an economically important
52 fishery both to local Alaskan fishers throughout the GOA and to other US West Coast commercial
53 fishers (Williams et al. 2020, Hulson et al. 2020). In 2020, 178,000 tons of groundfish was harvested
54 in the GOA, valued at \$92.9 million (Fissel 2020).

55 The groundfish management category includes fish species that are generally found on or near the
56 seabed of continental shelves, areas of the ocean that are less than 1000 meters deep and generally
57 occur just offshore of coastlines. In the commercial fishery, groundfish are harvested primarily with
58 bottom trawls (Williams et al. 2020, Hulson et al. 2020). It is fairly typical for groundfish stock
59 trawl hauls to produce a few very large catches while the majority of hauls catch very few or none
60 of a given stock, which may signify that these populations have a clustered spatial distribution. As
61 a result, their populations' abundance and distribution is particularly difficult to model.

62 A lot is still unknown about the biology and ecology of most groundfish species, which also contributes

63 to the challenge of modeling groundfish population dynamics. In the GOA, commercial groundfish
64 fishing exploded in the 1960s and 70s, and some stocks subsequently experienced significant decreases
65 in population (Williams et al. 2020, Hulson et al. 2020). While declines appear to be correlated
66 with increased fishing pressure and therefore could be caused by overfishing, it is not usually
67 possible to say definitively that a stock's decline is due directly to overfishing because there may be
68 coinciding environmental variables that contribute to a decline. Regardless of the reason, once a
69 population is clearly in decline, fisheries managers become concerned that the reduced population
70 may be vulnerable to overfishing at that point and the stock will be driven into even further decline.
71 Consequently, commercial fishing of groundfish in the GOA was regulated much more strictly
72 starting in the 1980s, and many of the stocks have experienced increases in population since then
73 (Williams et al. 2020, Hulson et al. 2020). Because of the declines and subsequent recoveries,
74 these stocks are managed carefully and improving modeling methods is a priority for management
75 (Williams et al. 2020, Hulson et al. 2020). Two groundfish stocks that experienced this decline
76 and have subsequently recovered are Pacific Ocean Perch (*Sebastes alutus*) and Northern Rockfish
77 (*Sebastes polypin*).

78 Pacific Ocean Perch and Northern Rockfish, like many groundfish species, are long lived and slow to
79 mature, therefore it is reasonable to assume that the population biomass in a healthy population
80 would not fluctuate an enormous amount from year to year (Davison et al. 2019). However, the
81 data collected every 2 or 3 years in the bottom trawl survey conducted by the National Oceanic &
82 Atmospheric Administration (NOAA) National Marine Fisheries Service's (NMFS) Alaska Fisheries
83 Science Center (AFSC) shows a fairly large amount of interannual variation. This is likely less to
84 do with true interannual changes in stock biomass and much more likely the result of low survey
85 sample sizes (particularly for Northern Rockfish) applied to what appears to be clustered population
86 distributions. In addition, there are logistical or data collection issues, particularly the inability to
87 trawl in many areas of the GOA due to rocky bottom habitat, that contribute to this variability.
88 Ideally, a statistical model that uses this survey data to predict stock biomass would seek to minimize
89 the impact of this artificial variability.

90 Many groundfish stocks in the GOA are managed by allocating harvest rules across three designated
91 subregions: western, central, and eastern GOA. Each subregion is allocated a proportion of the
92 stock's harvest limit in the GOA management decisions according to the proportion of the stock's
93 biomass that is estimated to occur in that subregion (Williams et al. 2020, Hulson et al. 2020).

94 The designation of these subregions is primarily used to ensure that local fishing communities
95 across the GOA have access to a sustainable population of fish. In this management approach,
96 there are two models used to estimate groundfish biomass: (1) an age-structured population model
97 that generates biomass estimates across the entire GOA and (2) a state-space random walk model
98 (hereafter referred to as random walk) that estimates the proportion of that biomass that occurs in
99 each subregion of the GOA (Williams et al. 2020, Hulson et al. 2020).

100 The random walk model that is currently used to estimate the proportion of stock biomass across
101 subregions for these stocks is a flexible model that has many advantages. However, a disadvantage of
102 the model is that it is quite sensitive to variability in the input data. As a result, the high variability
103 in the survey data causes high uncertainty in the model results and the biomass predictions are
104 therefore not very precise, particularly in years without survey data. This high interannual variability
105 makes it difficult for fishers to plan for each fishing season and requires managers to revisit harvest
106 rules each year. Additionally, harvest rules may need to be set lower than is likely needed to reduce
107 risk of overfishing. If the model produced more precise estimates, managers could potentially raise
108 catch limits with confidence in maintaining sustainable populations. Precision must be balanced with
109 accuracy, however, as estimates that are very precise but inaccurate may lead to either over-fishing
110 or under-harvesting.

111 As currently implemented, the random walk model does not use spatial information as a variable
112 and only the data from hauls caught in each subregion are used to fit the model to estimate the
113 biomass in that subregion. This means that a lot of data is being excluded that could potentially
114 be used to improve the precision or accuracy of the model. A spatiotemporal model that uses both
115 temporal and spatial variables has the potential to produce biomass proportion estimates with
116 increased precision or accuracy compared to the random walk.

117 In this study, I compare the ability of a spatiotemporal model to produce biomass proportion
118 estimates with more precision compared to the random walk model proportion estimates for Pacific
119 Ocean Perch and Northern Rockfish. In particular, an objective of this study is to determine if the
120 spatiotemporal model produces estimates with less interannual variability. In addition to improving
121 on precision, the spatiotemporal model needs to match or improve on the random walk model
122 biomass proportion estimates in terms of accuracy when compared to the survey data in order to be
123 considered a viable alternative.

124 **Methods**

125 **Species & study area**

126 This project focuses on two species, Pacific Ocean Perch (*Sebastes alutus*) and Northern Rockfish
127 (*Sebastes polyspinis*). These are two of the most economically important stocks in the GOA
128 commercial groundfish fishery, and they are managed as single species stocks with harvest allocated
129 by subregion. Pacific Ocean Perch alone has accounted for more than 60% of the catch in the GOA
130 groundfish fishery since 2015 (Williams et al. 2020, Hulson et al. 2020). In 2019 the catch for
131 Pacific Ocean Perch was worth \$23.9 million while Northern Rockfish catch was worth \$2.4 million
132 (Williams et al. 2020, Hulson et al. 2020).

133 Pacific Ocean Perch adults undergo a seasonal migration, where they move from deeper parts of the
134 continental shelf (300 - 420 meters) in the winter to shallower parts (150 - 300 m) in the summer.
135 They also move up higher in the water column during the day, likely to feed, and this may inflate
136 the variance associated with bottom trawl sampling if a substantial portion of the population is
137 absent from the bottom during trawling. Both Pacific Ocean Perch and Northern Rockfish are slow
138 maturing and long-lived, like most rockfish species; the oldest Pacific Ocean Perch and Northern
139 Rockfish individuals captured in the GOA were estimated to be 84 and 67 years old, respectively
140 (Williams et al. 2020, Hulson et al. 2020). Very little is known about the larval or juvenile stages of
141 either species, and even less is known about Northern Rockfish adult behavior than about Pacific
142 Ocean Perch adult behavior, other than the fact that they live up to their name and appear to
143 prefer rocky bottom habitat that is difficult to trawl (Williams et al. 2020, Hulson et al. 2020). This
144 lack of life history information contributes to the difficulty of modeling their population dynamics.

145 The study area in this analysis includes the continental shelf of the Gulf of Alaska, which is separated
146 into 3 management subregions: western, central, and eastern (Figure 1). The western and central
147 subregions are separated by -157° longitude and the central and eastern subregions are separated
148 by -147° longitude. The central subregion includes Kodiak Island, which is a significant source of
149 local Alaskan fishing activity.

150 *Bottom-trawl survey design*

151 The data for this study come from a bottom trawl survey carried out by AFSC that has been
152 operating in the GOA every 2 or 3 years since the 1980s. This is a multi-species survey that uses a

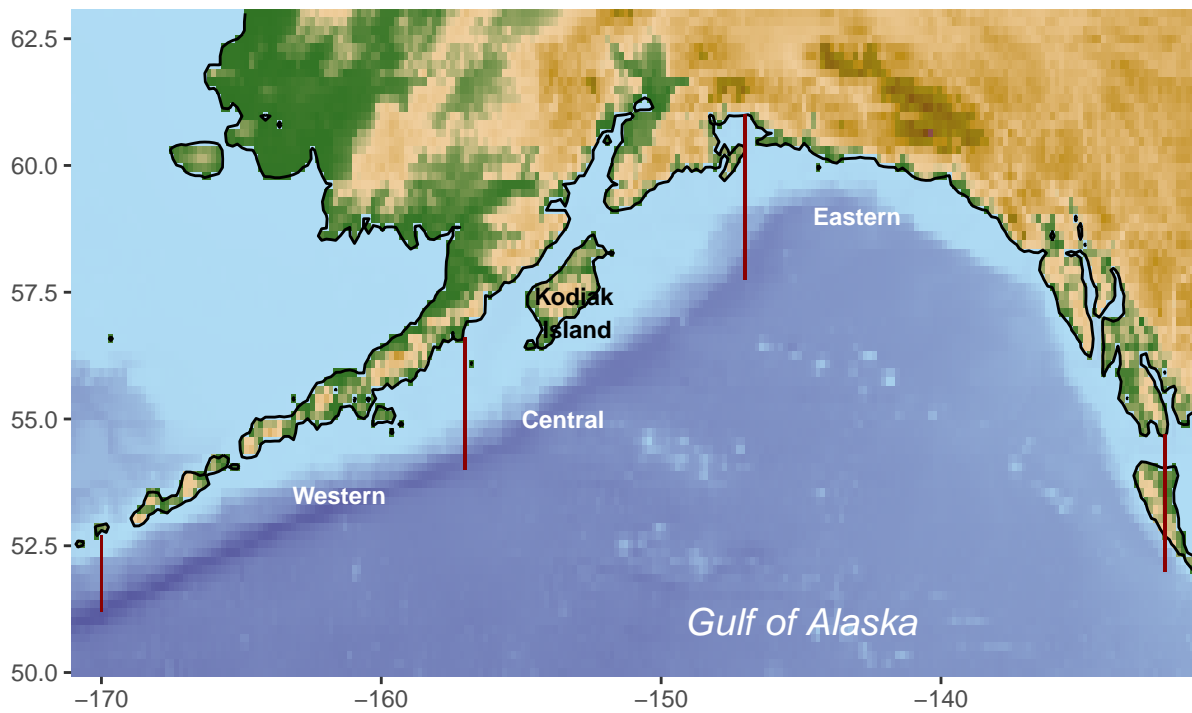


Figure 1: Map of the study area, the continental shelf of the Gulf of Alaska, shown in light blue. The three management subregions are delineated by red lines. The western edge of the western subregion is at -170° longitude and the furthest east edge of the eastern subregion is at -132.6° longitude.

153 spatially stratified random sampling method. The stratification used for this survey is primarily
 154 depth (with a maximum depth of 1000 m) with some influence from practicalities around logistical
 155 and economic considerations, and environmental features. A minimum of 2 primary sample locations
 156 is randomly selected for each depth strata each survey year (Stauffer 2004). When the primary
 157 sampling location is deemed untrawlable, a secondary location is randomized and sampling is
 158 attempted there. A significant challenge that this particular survey encounters is that large amounts
 159 of the bottom of the continental shelf are very rocky, making it difficult or impossible to trawl with
 160 the gear used by the survey (Stauffer 2004). The data for Pacific Ocean Perch used in this project
 161 start in 1990 and end in 2019 (14 years of survey data). The survey data for Northern Rockfish
 162 used in this project start in 1984 and end in 2019 (16 years of survey data).

163 **Model Descriptions**

164 *Random walk model*

165 In the implementation of the random walk model, the survey data are separated by subregion based
 166 on trawl haul location. The hauls in each subregion are then used to calculate a biomass per unit
 167 area surveyed, which is multiplied by the area of the subregion to produce a single value called
 168 the design-based estimate for each subregion in each year (y_t). A coefficient of variation for each
 169 subregion in each year is also calculated, using this design-based estimate and the variance of the
 170 catches in that subregion and year. The following steps are then performed for the data in each
 171 subregion separately.

172 The random walk model assumes that true biomass in year t (x_t) equals the true biomass in the
 173 year previous (x_{t-1}) plus process error (θ_p) from the previous year ($\theta_{p,t-1}$). The process error in
 174 a given year ($\theta_{p,t}$) is randomly drawn from a normal distribution with a mean of 0 and standard
 175 deviation, σ_p . The true biomass in the year before the first survey year, x_0 , and σ_p are estimated
 176 from the survey data. The model assumes stationarity in the process error, meaning that birth rates
 177 and death rates are expected to be fairly consistent through time for these species. Specifically,
 178 biomass is estimated by

$$x_t = x_{t-1} + \theta_{p,t-1} \qquad \theta_{p,t} \sim N(0, \sigma_p^2) \qquad (1.1)$$

179 The model further assumes that the design-based estimate in a given year (y_t) equals the true
 180 biomass for that year plus observation error in that year ($\theta_{o,t}$). Unlike process error, we assume
 181 that the amount of observation error may change from year to year, based on individual conditions
 182 in each year. A new observation error distribution is calculated for each year, with a mean of 0
 183 and a new variance ($\sigma_{o,t}^2$), taken from the coefficient of variation calculated with for survey data in
 184 each subregion in each year. In the case of these data, some likely contributors to observation error
 185 include the uncertainty associated with extrapolating sampled locations to unsampled locations
 186 given the likely clustered nature of the stocks' spatial distribution, and the fact that large portions
 187 of the bottom of the GOA are too rocky to trawl for this survey and may be preferred habitat for
 188 some or all of the species of interest. The observation model is

$$y_t = x_t + \theta_{o,t} \qquad \theta_{o,t} \sim N(0, \sigma_{o,t}^2) \qquad (1.2)$$

189 *Spatio-temporal model*

190 The spatio-temporal model I used is a hurdle model, specifically a delta-Generalized Linear Mixed
 191 Model (delta-GLMM) as described by Thorson (2017). The model uses a two-step process to
 192 predict stock biomass for each subregion. The first step is to determine whether the fish are in a
 193 particular area at a particular time (presence/absence). If no fish are present, the model estimates
 194 no biomass, regardless of the reason for absence (e.g., they are not present due to unsuitable habitat
 195 or seasonal/ontogenetic migration, they were present but the trawl did not capture them, or they
 196 were present and were captured but misidentified, etc). If the fish are present, then the second step
 197 is to estimate non-zero biomass at that place and time, also known as positive catch. The product
 198 of these two steps constitutes the delta-GLMM model.

199 The first equation represents encounter probability, the probability that the fish are present and at
 200 least 1 is sampled in a particular area at a particular time. The second equation predicts positive
 201 catch, the positive number of fish that can be caught in that area and time. Both equations use time,
 202 space and the interaction between time and space as variables. Positive catch is used to construct a
 203 gamma distribution representing observation error (as described for the Compound Poisson-Gamma
 204 model in Thorson 2017 (Thorson 2017)) and this is multiplied with encounter probability to produce
 205 an estimated biomass at time t and location s .

206 The encounter probability of observation i at location s and time t ($p_{i,s,t}$) is based on a function
 207 with both random and fixed effects ($n_{i,s,t}$), with an offset for area ($a_{i,s,t}$).

$$p_{i,s,t} = 1 - \exp(-a_{i,s,t} \times n_{i,s,t}) \quad (2)$$

208 $n_{i,s,t}$ is subject to a log-link and is made up of an autocorrelated temporal random or fixed effect
 209 (depending on species), $\beta_{1,t}$, a spatial random effect, $\nu_{1,s}$, and a spatio-temporal random effect, $\epsilon_{1,s,t}$,
 210 as shown below.

$$\log[n_{i,s,t}] = \beta_{1,t} + \nu_{1,s} + \epsilon_{1,s,t} \quad (3.1)$$

211 Both the spatial and spatio-temporal variables are drawn from multivariate normal distributions
 212 with means of 0 and variance-covariance matrices made up of two parts:

$$\begin{aligned} \nu_1 &\sim \text{MVN}(0, \sigma_{1\nu}^2 \mathbf{R}) \\ \epsilon_1 &\sim \text{MVN}(0, \sigma_{1\epsilon}^2 \mathbf{R}) \end{aligned} \quad (3.2)$$

213 The \mathbf{R} term in the variance-covariance matrices is a matrix of the spatial correlations for the entire
 214 area given an estimated distance κ . The other part of the variance-covariance matrices, $\sigma_{1\nu}^2$ and
 215 $\sigma_{1\epsilon}^2$, are the estimated pointwise variances of spatial variation in the observations for $\nu_{1,s}$ and $\epsilon_{1,s,t}$,
 216 respectively (see Thorson and Barnett 2017 for a full description of the spatial method).

217 Initially both species were fit with $\beta_{1,t}$ set as a random walk. However, for Northern Rockfish the
 218 resulting parameter estimates were extremely small. Consequently, the temporal random effect is
 219 configured differently for each species. For Pacific Ocean Perch, $\beta_{1,t}$ is a random walk, with t_{min} as
 220 the first survey year:

$$\beta_{1,t} \sim \begin{cases} \text{N}(0, 1) & \text{if } t = t_{min} \\ \text{N}(\beta_{1,t-1}, 1) & \text{if } t > t_{min} \end{cases} \quad (3.3)$$

221 For Northern Rockfish, $\beta_{1,t}$ is a fixed intercept and constant among years.

222 The second equation of the model represents positive catch ($w_{i,s,t}$), subject to a log-link and made

223 up of a temporal random effect ($\beta_{2,t}$), a spatial random effect ($\nu_{2,s}$) and a spatio-temporal random
 224 effect ($\epsilon_{2,s,t}$). The spatial and spatio-temporal random effects are calculated in the same way as the
 225 corresponding encounter probability equations and with similar variable definitions. The temporal
 226 random effect, $\beta_{2,t}$ is a random walk for both species, specified in the same way as the $\beta_{1,t}$ for Pacific
 227 Ocean Perch.

$$\log[w_{i,s,t}] = \beta_{2,t} + \nu_{2,s} + \epsilon_{2,s,t} \quad (4.1)$$

$$\begin{aligned} \nu_2 &\sim \text{MVN}(0, \sigma_{2\nu}^2 \mathbf{R}) \\ \epsilon_2 &\sim \text{MVN}(0, \sigma_{2\epsilon}^2 \mathbf{R}) \end{aligned} \quad (4.2)$$

228 Model evaluation

229 I created replicate data sets from the source data using jackknife resampling to produce multiple
 230 model results for a more robust comparison of model performance. For each replicate created
 231 through resampling, one year was excluded from the data. In 2001, the survey wasn't conducted in
 232 the eastern subregion, and the proportion calculation for the three subregions with the survey data
 233 was impossible for that year. I therefore omitted 2001 from both the survey data and model results,
 234 leaving 13 sets of model results for Pacific Ocean Perch (for 1990, 1993, 1996 and odd years from
 235 1999 - 2019) and 15 for Northern Rockfish (for 1984, 1987, 1990, 1993, 1996 and odd years from
 236 1999 - 2019) available to calculate the model evaluation metrics.

237 The delta-GLMM and random walk models were fit with each replicate dataset for each species.
 238 The estimated biomasses in subregion c in year t ($b_{c,t}$) were then used to calculate the proportion of
 239 estimated biomass from each model in subregion c in year t ($P_{c,t}$), with C indicating the number of
 240 subregions.

$$P_{c,t} = \frac{b_{c,t}}{\sum_{c=1}^C b_{c,t}} \quad (5)$$

241 The proportion of biomass in each subregion in each year from the survey data ($P_{d,c,t}$) was calculated
 242 in the same way, and will be referred to hereafter as the design-based proportion.

243 For the metrics described below, the calculations are all done with the model estimates for the

244 jackknifed year in each dataset, hereafter referred to as the jackknife estimate or jackknife proportion
 245 estimate, with subscript e for year equations. This allows a comparison to be made both between
 246 how precise a model estimate is when data are excluded compared to when they are included (a
 247 year t subscript refers to the model estimate from the version that included all data). Additionally,
 248 it shows the maximum amount of difference in accuracy and precision that the model introduces
 249 when data don't exist when compared to the design-based proportion.

250 Accuracy was measured using an absolute difference ($D_{c,e}$) between the jackknife proportion estimate
 251 in subregion c and excluded year e ($P_{r,c,e}$) and the design-based proportion estimate for that year.
 252 For example, the jackknife proportion estimate for 1990 from the replicate that excluded the data
 253 for 1990 is compared to the design-based proportion for 1990. The closer $D_{c,e}$ is to 0, the more
 254 accurate the model results are compared to the design-based proportion.

$$D_{c,e} = |P_{r,c,e} - P_{d,c,e}| \quad (6)$$

255 I also compared the jackknife estimates to the design-based estimates directly through plotting to
 256 look for indications of consistent bias in the model proportion estimates. This comparison was done
 257 with a simple regression of $P_{r,c,e} = m * P_{d,c,e} + b$, using a reference line of $y = x$, to see if the models
 258 were consistently over- or underestimating compared to the survey proportion. Overestimates
 259 occur above the reference line and underestimates occur below the line. In a management context,
 260 overestimating stock biomass could lead to overfishing by failing to detect when a stock has reached
 261 an unsustainable population level while underestimating stock would result in lost income for fishers
 262 and fishing communities.

263 To measure precision, I calculated a coefficient of variation ($CV_{c,e}$) for subregion c and excluded
 264 year e using the jackknife proportion estimate described above ($P_{r,c,e}$) and the standard error of
 265 that proportion ($SE[P_{r,c,e}]$).

$$CV_{c,e} = \frac{SE[P_{r,c,e}]}{P_{r,c,e}} \quad (7)$$

266 The standard error of the model estimated proportion ($SE[P_{r,c,e}]$) was approximated using a method
 267 from Thorson and Haltuch (2018) that uses the estimated biomass in subregion c in year e ($b_{c,e}$),
 268 the sum of all subregional estimated biomasses for each year (B_e), and the estimated standard error

269 of the biomass in subregion c in year e ($SE[b_{c,e}]$).

$$SE[P_{r,c,e}]^2 \approx \frac{b_{c,e}^2}{B_e^2} \left[\frac{SE[b_{c,e}]^2}{b_{c,e}^2} - 2 \frac{SE[b_{c,e}]^2}{b_{c,e} B_e} + \frac{\sum_{c=1}^C SE[b_{c,e}]^2}{B_e^2} \right] \quad (8)$$

270 The mean jackknife CV value and the distribution of jackknife CVs was examined for each subregion,
271 with more precision indicated by CV values being closer to zero. In addition, I calculated the
272 ratio between the CV value calculated for jackknife CVs ($CV_{c,e}$) with the CV value calculated for
273 that year t for subregion c in the model results version that included all of the data ($CV_{c,t}$). This
274 comparison showed how much relative uncertainty estimating a year without data introduces for
275 each model.

$$\frac{CV_{c,e}}{CV_{c,t}} \quad (9)$$

276 In order to quantify how well the standard errors of the proportion provided coverage for the difference
277 between the jackknife estimates and the design-based estimates, I calculated that difference divided
278 by the jackknife standard error.

$$\frac{P_{r,c,e} - P_{d,c,e}}{SE(P_{r,c,e})} \quad (10)$$

279 I then used the `pnorm` function in R to determine what the probability of these values occurring
280 would be if they came from a normal distribution, with the expectation that good coverage would
281 be approximately characterized by a normal distribution. I visually compared the histogram of the
282 `pnorm` values with a normal curve (with mean = 0.5 and standard deviation = 0.16 to approximate
283 a normal distribution on a 0 to 1 scale) to evaluate whether the models produced roughly normal-
284 looking coverage. If the `pnorm` coverage values occur more frequently outside the bounds of the
285 normal curve, then this would indicate that the jackknife standard errors are frequently very small
286 compared to the difference between the jackknife estimate and the design-based estimate, and
287 precision may be too high to compensate for the model's level of accuracy.

288 Finally, the delta-GLMM model was used to predict the proportion of biomass in each subregion for
289 each species in 2020, 2021 and 2022. These predictions were then used to compare how different
290 proportions estimated from the delta-GLMM model would be compared to the random walk for

291 how total allowable catch (TAC) would be allocated by subregion for 2020 - 2022. This was done
292 using the total biomass estimated for 2020, 2021 and 2022 by the age-structured model in the stock
293 assessments.

294 **Results**

295 The majority of Northern Rockfish biomass is found in the western and central subregions, with less
296 than one percent occurring in the eastern subregion, according to both the design-based proportion
297 and both models' estimates. Due to this very minimal presence, the NOAA AFSC stock assessment
298 only allocates catch to the western and central subregions. Accordingly, in this analysis the eastern
299 subregion was excluded from the model comparison metrics for Northern Rockfish, while results for
300 Pacific Ocean Perch were evaluated for all three subregions.

301 The random walk model results roughly follow the trajectory of the design-based proportion across
302 all subregions in terms of the proportion of biomass across the timeseries for both Pacific Ocean
303 Perch and Northern Rockfish (Figure 2). The delta-GLMM model shows less fluctuation between
304 years than either the random walk model or the design-based proportions for both species, but
305 consequently it deviates from the design-based estimates more than the random walk model does.
306 There is a much more dramatic difference between the delta-GLMM estimates and the design-based
307 estimates occurring for Northern Rockfish than for Pacific Ocean Perch.

308 According to both models and the design-based proportion, the proportion of total biomass for
309 Pacific Ocean Perch has decreased in the western subregion, starting around 20% of biomass in 1990
310 and decreasing to less than 10% in 2019, with a brief spike in proportion up to as much as 25%
311 between 2005 and 2007. In the central subregion, it has increased, from between 30-40% in 1990
312 (with delta-GLMM predicting the higher proportion), with more than 50% of biomass found in
313 that subregion since 1993, and up to approximately 75% in 2019, according to both models and the
314 design-based proportion. In 1990, more than 40% of the biomass was in the eastern subregion but
315 that sharply decreased between 1990 and 2000 to less than 20% according to the random walk model
316 and design-based proportion, although the delta-GLMM estimated approximately 25% between
317 1993 and 2000. Since 2000, the eastern subregion proportion has been maintained at approximately
318 20-25% of the total biomass according to both models and the design-based proportion. The largest
319 difference between the delta-GLMM and the design-based and random walk estimates occurred

320 between 1996 and 2003, when there was a relatively large fluctuation in the design-based proportion
321 for all subregions (increasing in the central subregion and decreasing in the other two subregions,
322 particularly in eastern) that the delta-GLMM did not follow.

323 For Northern Rockfish, the delta-GLMM model estimates follow the trajectory of the design-based
324 proportion until 1996, when a large departure occurs for the delta-GLMM results (Figure 2). From
325 1999 to 2019, the delta-GLMM results estimate that consistently 50-70% of the Northern Rockfish
326 biomass occurs in the western subregion while 30-50% occurs in the central subregion. In contrast,
327 the design-based proportion and the random walk results fluctuate much more, with between 20 -
328 65% of the biomass in western and 35 - 80% in central.

329 **Accuracy Metrics**

330 When the design-based proportion estimate is directly compared to the jackknife proportion estimate
331 for Pacific Ocean Perch, neither the random walk nor the delta-GLMM appear to consistently
332 over- or underestimate for the western subregion (Figure 3). The delta-GLMM appears to slightly
333 underestimate the proportion in the central subregion while more clearly overestimating in the
334 eastern subregion. The random walk does not tend towards over- or underestimation for any of
335 the subregions, but has a fairly even spread of values above and below the reference line. Both
336 models produce estimates that are fairly tightly clustered around the reference line for all subregions,
337 indicating that both models' estimates are fairly close to the design-based proportion in all subregions.

338 The direct comparison of the jackknife estimate with the design-based estimate for Northern Rockfish
339 reveals that the delta-GLMM consistently overestimates in the western subregion and underestimates
340 in the central subregion (Figure 3). The random walk estimates are more evenly spread, indicating
341 no consistent over- or underestimation. However, both model estimates show a wide spread from
342 the reference line, indicating that the estimates from both models diverge much more from the
343 survey proportion than occurred with Pacific Ocean Perch.

344 The random walk model had lower mean absolute difference values for all three subregions than the
345 delta-GLMM for Pacific Ocean Perch (Table 1). However, in all cases the difference between the
346 means for the two models was quite small, and the distribution of the absolute difference values
347 shows a lot of overlap between the two models (Figure 4). The two models appear to have a similar
348 level of accuracy to the design-based proportion based on this metric. Similarly, for Northern
349 Rockfish the random walk model has a lower mean absolute difference than the delta-GLMM for

350 both subregions (Table 1) but the histograms of all of the absolute difference values show a lot of
351 overlap (Figure 4). Based on these results, neither model has a clear advantage over the other in
352 terms of accuracy for either species. The absolute difference values for both models are a greater
353 magnitude for Northern Rockfish than for Pacific Ocean Perch, indicating that both models had
354 more accurate estimates for Pacific Ocean Perch than for Northern Rockfish.

355 **Precision Metrics**

356 The delta-GLMM model had lower mean jackknife CV ($CV_{c,e}$) values than the random walk for
357 both Pacific Ocean Perch and Northern Rockfish (Table 1). The distribution of jackknife CV values
358 also shows that the delta-GLMM has lower values for almost all years in the western and eastern
359 subregions for Pacific Ocean Perch and the western subregion for Northern Rockfish (Figure 5). The
360 central subregion shows more overlap between models for both species, with a smaller difference
361 between their mean CV values than the other subregions. The ratio of the jackknife CV with the
362 CV calculated from the data set using all years revealed that the delta-GLMM model had more
363 consistent and smaller CV ratios, indicating that excluding a year of data increase uncertainty
364 more for the random walk model than the delta-GLMM (Figure 6). The exception to this trend
365 is the CV ratios for 1990, 1993, 1996 and 1999 for Pacific Ocean Perch in the central and eastern
366 subregions and 2005 for Northern Rockfish in both subregions, where the delta-GLMM had a greater
367 increase in uncertainty when each of those years was excluded than the random walk model. Both
368 species' results shows that the random walk model has a higher increase of uncertainty than the
369 delta-GLMM when the most recent survey year (2019) is excluded.

370 A visual evaluation of the coverage of the jackknife standard errors relative to the difference between
371 the jackknife estimates and the design-based estimates showed that the delta-GLMM results did
372 not conform to a normal curve much more than the random walk results for both species (Figure
373 7). While the random walk results do not exactly look like a normal distribution either, there are
374 far fewer coverage values that fall entirely outside of the normal curve, while the majority of the
375 delta-GLMM values occurred outside the curve.

376 **2020 - 2022 Total Allowable Catch**

377 The delta-GLMM model produced TAC allocations for 2020 - 2022 that were somewhat different to
378 the allocations generated by the random walk model for Pacific Ocean Perch (Table 2). The biggest
379 difference was seen in the western subregion, where the delta-GLMM allocated higher biomass by

380 between 850 - 950 mt, representing an approximately 60-64% increase because the allocation in
381 that subregion is fairly small. In the eastern subregion, the delta-GLMM allocated between 50 and
382 275 mt more, representing only a 1-5% increase, and between 900 and 1,100 mt less to the central
383 subregion (3-5% decrease) compared to the random walk model.

384 The difference between the delta-GLMM proportion predictions for 2020 - 2022, and how that would
385 affect the TAC allocated to each subregion, is more dramatic for Northern Rockfish than for Pacific
386 Ocean Perch (Table 2). The delta-GLMM estimates that a greater proportion of the population
387 occurs in the western subregion while the random walk model and the design-based proportion
388 estimates that the greater proportion occurs in the central subregion. In terms of metric tons, this
389 means that between 1,300 and 1,600 mt would be shifted from the central subregion allocation to
390 the western allocation in all 3 years. In 2020, this would shift 37.5% of the TAC from central to
391 western, and in 2021 and 2022 it would shift approximately 26% of the TAC.

392 Discussion

393 The primary objective of this study was to use Pacific Ocean Perch and Northern Rockfish to
394 explore whether the delta-GLMM model could be used instead of the random walk model to more
395 precisely predict the proportion for groundfish species in each management subregion for the Gulf
396 of Alaska, while matching or exceeding the accuracy of the random walk model estimates. Based
397 on these results, the delta-GLMM has proved fairly equivalent in accuracy to the random walk
398 model for Pacific Ocean Perch while the random walk is somewhat more accurate for Northern
399 Rockfish, according to the proportion absolute difference metric ($D_{c,e}$). The metrics for precision,
400 the jackknife CV ($CV_{c,e}$) and the ratio of those CVs with the CV for the model results using all
401 data ($CV_{c,t}$), both indicate that the delta-GLMM is more precise than the random walk for both
402 species, as expected.

403 However, the delta-GLMM showed some instances of possible bias in its estimates, particularly for
404 Northern Rockfish. Additionally, it appears that the jackknife standard errors of the delta-GLMM
405 are too small to cover the difference between the jackknife estimates and the design-based estimates
406 much more frequently than would be expected if the coverage was normally distributed. The
407 random walk model, however, does appear to approximately fit a normal distribution for its coverage.
408 Consequently, although the delta-GLMM model technically meets the stated criteria to be considered

409 as an alternative to the random walk model (increased precision and at least equal accuracy), it
410 may not be a good alternative in this form, as there is a greater risk of over- or under-estimating
411 subregional population proportion compared to the random walk model.

412 Another objective of this study was to investigate if the delta-GLMM model produces results with
413 a lower interannual variability than the random walk model. This does appear to be the case, as
414 the delta-GLMM smooths estimates more than the random walk - this is particularly clear in the
415 Northern Rockfish results in figure 2. This is an expected result, as the delta-GLMM is performing
416 spatial smoothing while the random walk is not. However, the issue of overly small precision also
417 affects this objective. While this objective is technically being met by the delta-GLMM model,
418 particularly for Northern Rockfish, the greater difference between the model estimated proportions
419 and the design-based proportion due to the smoothing is not covered enough of the time by the
420 proportion standard errors, and over- or underestimation occurs too frequently.

421 It is interesting to note that in Figure 6 the delta-GLMM model shows consistent decreased
422 uncertainty for Pacific Ocean Perch when data are excluded when surveys occur every other year as
423 opposed to every 3 years (as was the case up until 1999), while the random walk model appears
424 to vary in increased uncertainty regardless of whether the survey occurs every 3 or every 2 years.
425 Northern Rockfish, on the other hand, showed more variation in the amount of uncertainty introduced
426 by excluding a year of data regardless of whether the survey occurred every 2 vs 3 years. However,
427 there was a consistently higher level of uncertainty introduced into results for the random walk
428 model excluding 2019, the most recent survey year, for both species while the delta-GLMM model
429 had about the same change in uncertainty when excluding 2019 as any of the previous several years.
430 This result may be significant because the purpose of these models is to predict biomass proportion
431 by subregion up to 3 years into the future, so based on these results the delta-GLMM may introduce
432 less uncertainty in predictions of at least 2 years into the future than the random walk model for
433 Pacific Ocean Perch. The assumption that the delta-GLMM would provide projections into the
434 future with lower uncertainty appears to be supported by these results, and may indicate that
435 further experimentation with the delta-GLMM model as an alternative to the random walk model
436 is worth pursuing.

437 **Assumptions & limitations of the study**

438 A key assumption of this study is that the bottom trawl survey data are representative of the realistic
439 population distribution across subregions. While this assumption is useful for the purposes of this
440 study because it allows the two models to be compared with an accuracy metric, the survey is likely
441 to be an imprecise representation of the annual distribution and abundance of the populations. If
442 the survey data were believed to be truly representative on its own, then the design-based proportion
443 estimates could be used directly to set subregional TAC, rather than using a statistical model. In
444 this case, based on what we know of the life history of long-lived species like Pacific Ocean Perch
445 and Northern Rockfish, the high amount of interannual variation seen in the survey data is unlikely
446 to be an accurate representation of the population. An underlying clustered spatial distribution that
447 is being unevenly sampled may be part of the reason for this variability, combined with the issue
448 of a portion of the bottom of the GOA being untrawlable with the survey nets due to rockiness.
449 The assumption inherent in the design-based proportions is that the samples of catch from trawled
450 habitat can be extrapolated into the untrawlable habitat, and if these rocky areas are preferred
451 habitat for some rockfish, such as Northern Rockfish, this assumption may be inaccurate.

452 In addition to untrawlable bottom and clustered spatial distributions, Pacific Ocean Perch are
453 known to spend some amount of time in the pelagic zone (likely feeding), and consequently a survey
454 consisting only of bottom trawl gear may miss some percentage of the population depending on the
455 timing of the trawl and the movements of the fish. Since 2006, an average of 31% of the commercial
456 catch for Pacific Ocean Perch came from pelagic trawl rather than bottom trawl methods, up from
457 an average of 7% from 1990 - 2005 (Hulson et al. 2020). This increase in percentage of catch in
458 pelagic hauls in the commercial fishery seems more likely to be due to changes in practices or gear
459 in the fishery rather than increasing numbers of Pacific Ocean Perch occurring in the pelagic zone,
460 but the fact remains that some portion of the population may not be available to the bottom trawl
461 survey and this may need to be accounted for.

462 Pacific Ocean Perch and Northern Rockfish were the stocks chosen for this study because of their
463 high economic value in the GOA groundfish fishery. However, these stocks may be particularly
464 difficult to fit with the delta-GLMM model due to the very large catches that can occur with these
465 stocks, leading to significant changes in abundance estimates from year to year. Therefore the
466 results of this study may not be applicable to other groundfish stocks in the GOA. Consequently, a

467 similar comparison study pursued with other stocks may yield different results.

468 **Future research opportunities**

469 There are multiple directions for future study opportunities, including addressing the issue of how the
470 accuracy of the design-based proportions relative to the true population distributions affects model
471 performance, modifying the delta-GLMM model to improve accuracy, or modifying the random
472 walk model to decrease uncertainty. The issue of how the accuracy of the design-based proportions
473 relative to the true population distribution affects model performance could be addressed using a
474 simulation experiment where simulated survey data are created from age-structure populations with
475 a gradient of accuracy compared to the underlying population distribution. The models can then be
476 fit to these simulated data sets to see how much the accuracy of the survey affects model performance
477 and if one model performs better than the other as accuracy of the survey data decreases.

478 There are several avenues that could be explored to modify the delta-GLMM model. A strength of
479 the delta-GLMM is that other variables can be added into either or both equations, so environmental
480 factors like bottom type (rocky, sandy, etc.) and various types of temperature-related covariates could
481 be included in future versions of the model. Incorporating environmental covariates into the model
482 are likely to be particularly valuable in light of likely climate change-driven environmental changes
483 in the GOA, and may assist with predicting distributional shifts that may occur with changing
484 environmental conditions. The delta-GLMM model has been used to incorporate environmental
485 covariates for estimating stock distributions in the Bering Sea, and this would be a valuable avenue
486 to explore for future studies (Brodie et al. 2020, O’Leary et al. 2020) . The delta-GLMM model can
487 also be used to incorporate multiple types of data sources, including eDNA, acoustic, underwater
488 drop-camera data, and industry surveys. Future studies could use these alternate data sources to
489 improve inference into untrawlable habitat and improve model performance.

490 Other options for modifying the delta-GLMM model in future studies could include experimenting
491 with using a more flexible Tweedie distribution for the observation error in the delta-GLMM model
492 rather than the gamma distribution. This was initially attempted in this study, but for Northern
493 Rockfish in particular there were issues with finding appropriate starting values for the model, and
494 convergence issues even if viable starting values were identified. The decision was therefore made to
495 concentrate on the simpler gamma distribution for this study. A possible reason for this is that

496 the Tweedie distribution requires more parameters, and for the Northern Rockfish in particular the
 497 data set may not be large enough to adequately estimate additional parameters.

498 Alternatively, future studies could explore how to improve the precision of the random walk model
 499 by adding an informed prior for the process error variance. Based on what is currently known about
 500 the life history of long-lived species, this variance is likely to be fairly low and would likely lead to
 501 decreased uncertainty of the model estimates.

502

503 **Tables & Figures**

504 Table 1. Summary of average absolute difference and jackknife CV values for estimated excluded
 505 years (n = 13 for Pacific Ocean Perch, n = 15 for Northern Rockfish).

506

Species	Subregion	Model	Absolute Difference	CV
Pacific Ocean Perch	WESTERN	Random Walk	0.0667	0.6468
		delta-GLMM	0.0757	0.2411
	CENTRAL	Random Walk	0.1085	0.2155
		delta-GLMM	0.1218	0.1108
	EASTERN	Random Walk	0.0700	0.3841
		delta-GLMM	0.0918	0.1814
Northern Rockfish	WESTERN	Random Walk	0.1497	0.9067
		delta-GLMM	0.2357	0.2153
	CENTRAL	Random Walk	0.1497	0.4173
		delta-GLMM	0.2357	0.2263

507 Table 2. Comparing estimated predictions for 2020, 2021 and 2022 from delta-GLMM and the
508 random walk for each species and subregion in metric tons, using the estimated total biomass for
509 each year in the 2020 stock assessment multiplied by the model predicted proportion. The estimated
510 biomass per subregion for the random walk model was also taken from the stock assessment, since
511 that is the method currently used. The single ton of Northern Rockfish catch allocated in the
512 eastern subregion has historically been added into the multispecies “Other Rockfish” stock TAC
513 (Hulson et al. 2020), and the delta-GLMM proportion estimates would not change this practice.

Year	Metric tons			Source
	Western	Central	Eastern	
Pacific Ocean perch				
2020	1437	23678	6123	Random Walk
2020	2285	22550	6403	delta-GLMM
2021	1643	27429	7105	Random Walk
2021	2609	26344	7224	delta-GLMM
2022	1572	26234	6796	Random Walk
2022	2465	25380	6756	delta-GLMM
Northern Rockfish				
2020	1133	3178	1	Random Walk
2020	2749	1561	1	delta-GLMM
2021	2023	3334	1	Random Walk
2021	3439	1919	1	delta-GLMM
2022	1926	3173	1	Random Walk
2022	3290	1809	1	delta-GLMM

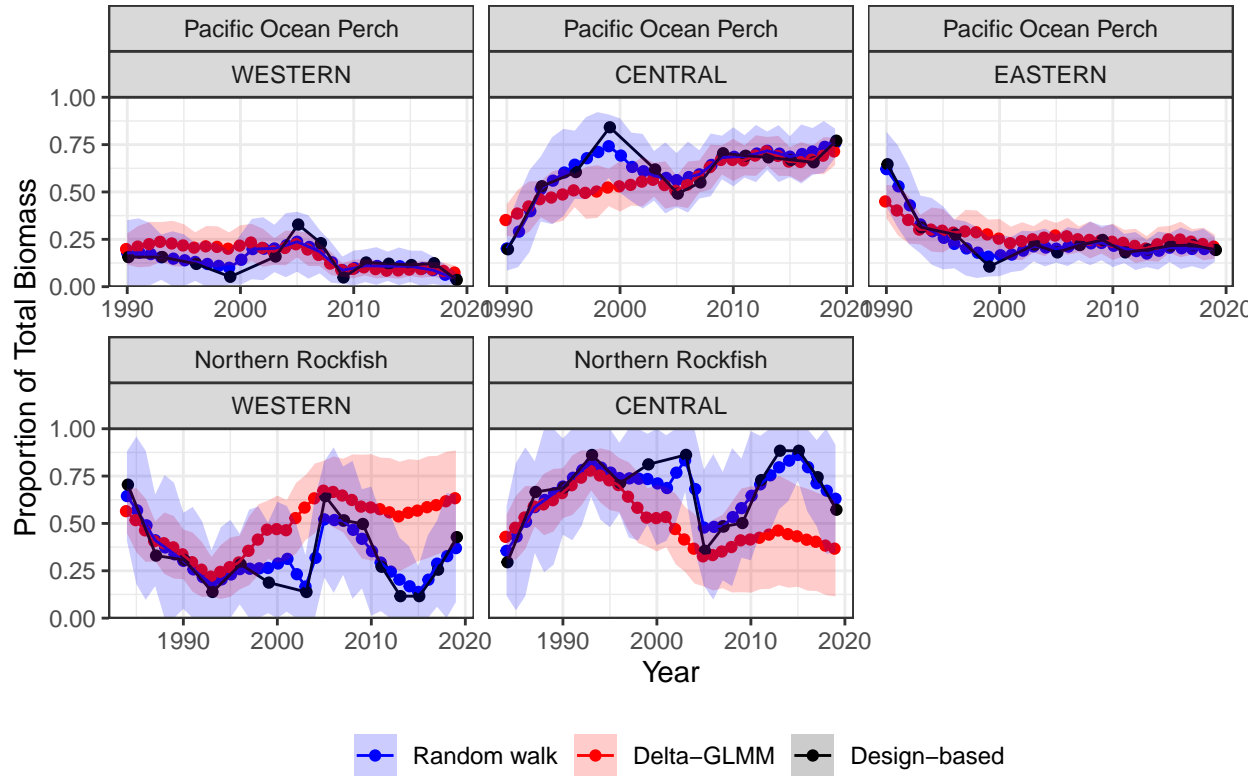


Figure 2: Estimate of proportion for each year using the random walk model (blue) and delta-GLMM model (red), showing both estimates (points) and ± 2 estimated standard error (colored ribbons), along with the design-based proportions (black bullets) for each region and species. Model estimates shown are the results calculated with all years of data (no years excluded).

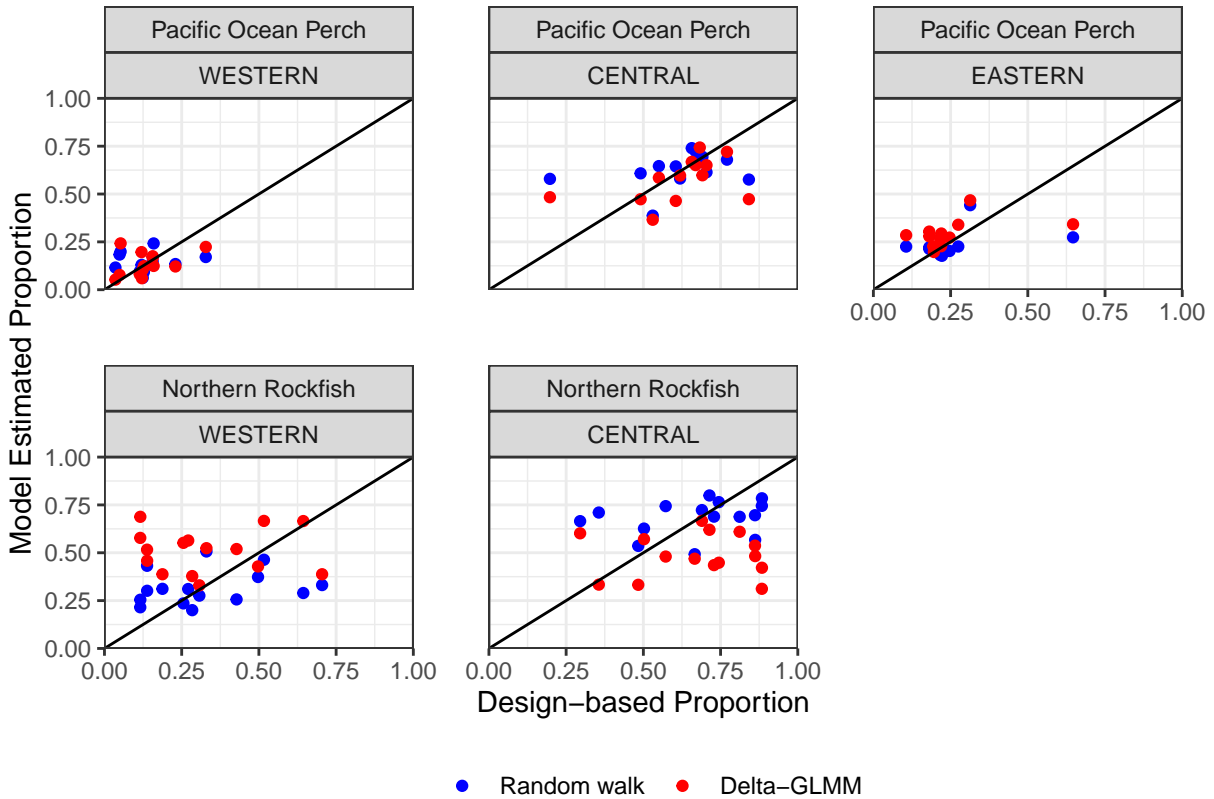


Figure 3: Design-based proportion estimate against jackknife proportion estimate for the random walk (blue plots) vs. delta-GLMM (red points) for each subregion and species. The black lines mark the reference line $y = x$, where the design-based estimate would be the same as the jackknife estimate.

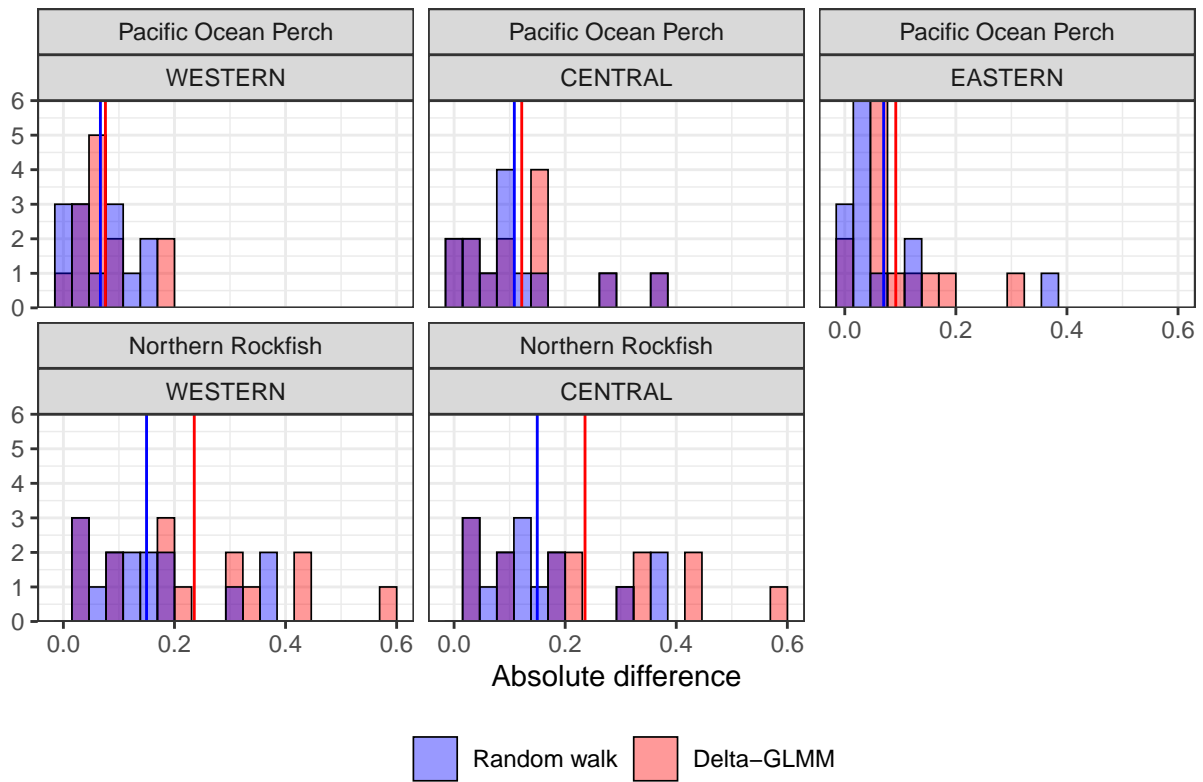


Figure 4: Histogram of absolute difference between the jackknife proportion estimates relative to the design-based proportion estimates, comparing the random walk (blue shading) vs. delta-GLMM (red shading) models. The mean absolute difference for the random walk model is shown with the blue line and the mean absolute difference for the delta-GLMM model is shown with the red line.

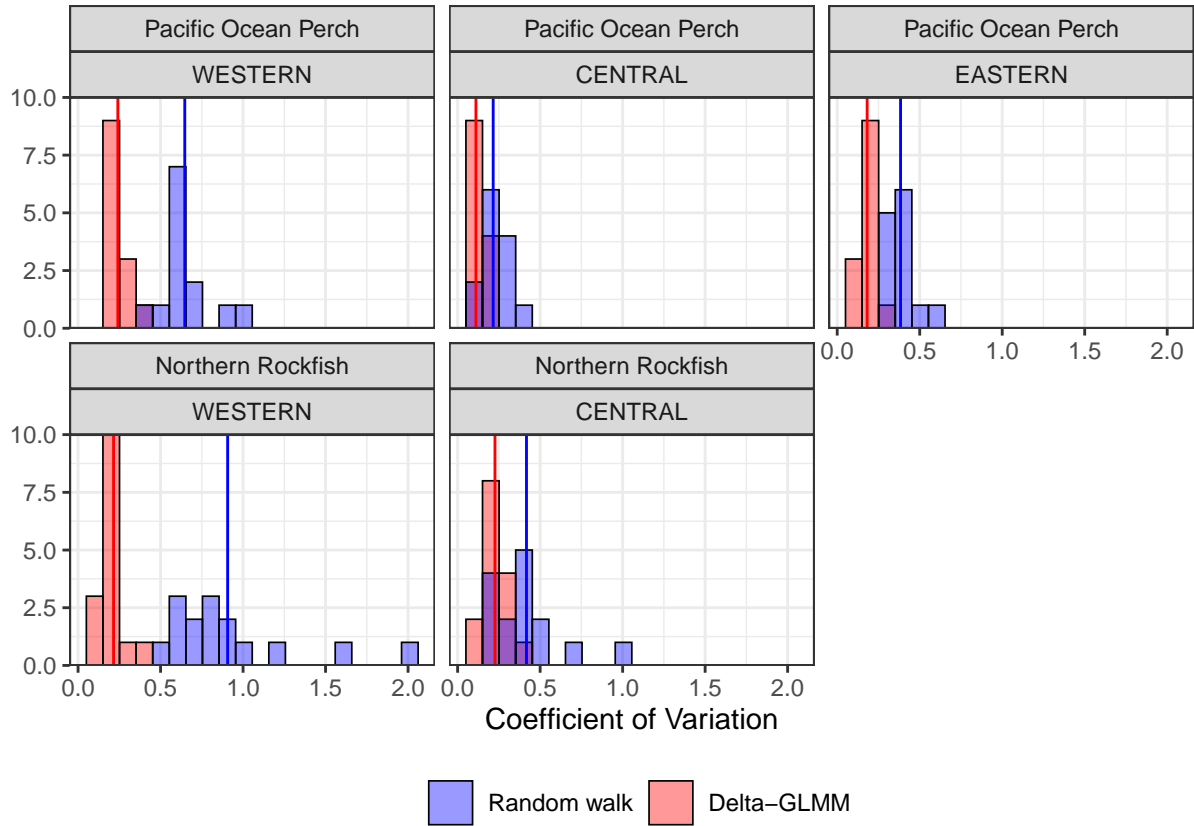


Figure 5: Histogram of CV values for random walk (blue shading) and delta-GLMM (red shading) results, calculated with the jackknife proportion estimates and jackknife standard errors (resulting in 13 values for Pacific Ocean Perch, 15 for Northern Rockfish). The mean CV for the random walk model is shown with the blue line and the mean CV for the delta-GLMM model is shown with the red line.

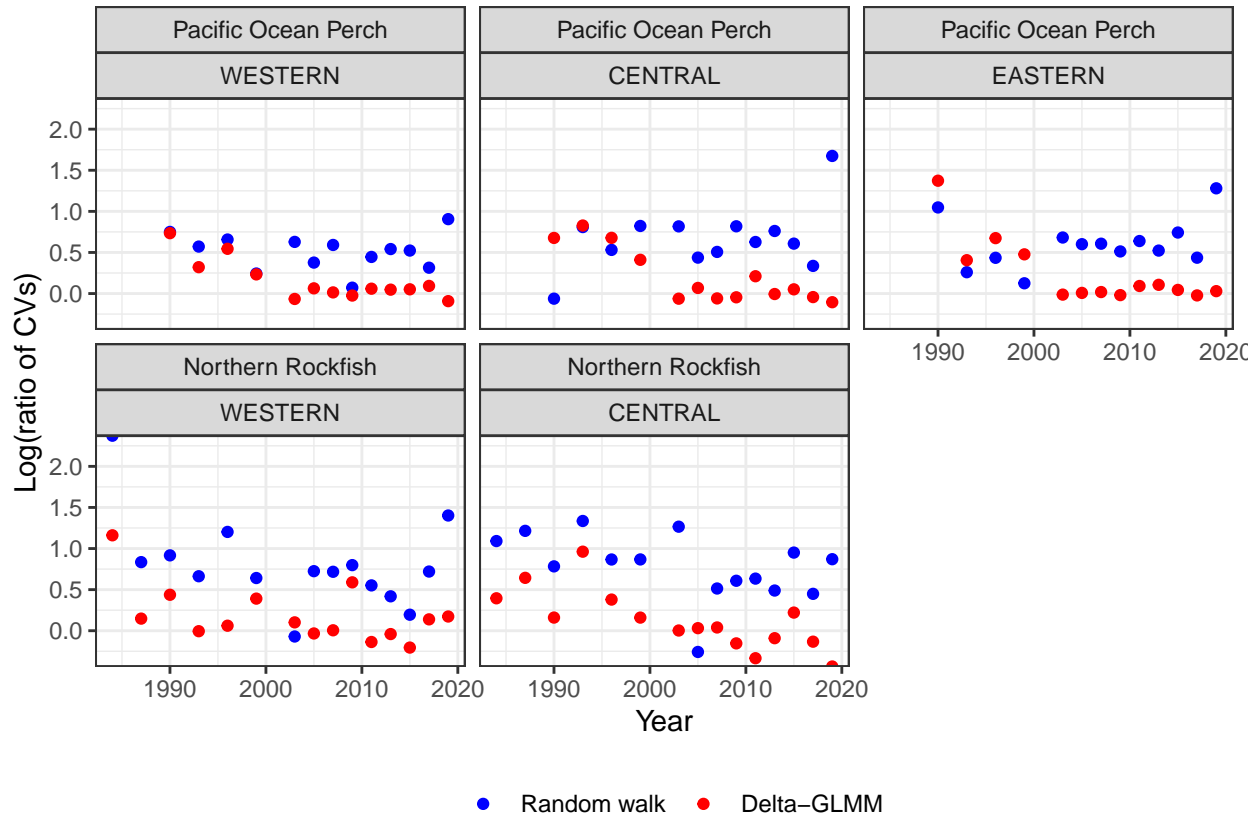


Figure 6: Histogram of the ratio of jackknife CVs ($CV_{c,e}$) to the CV calculated with all years' data included ($CV_{c,t}$), on log scale. The random walk values are shown in blue and the delta-GLMM values are in red.

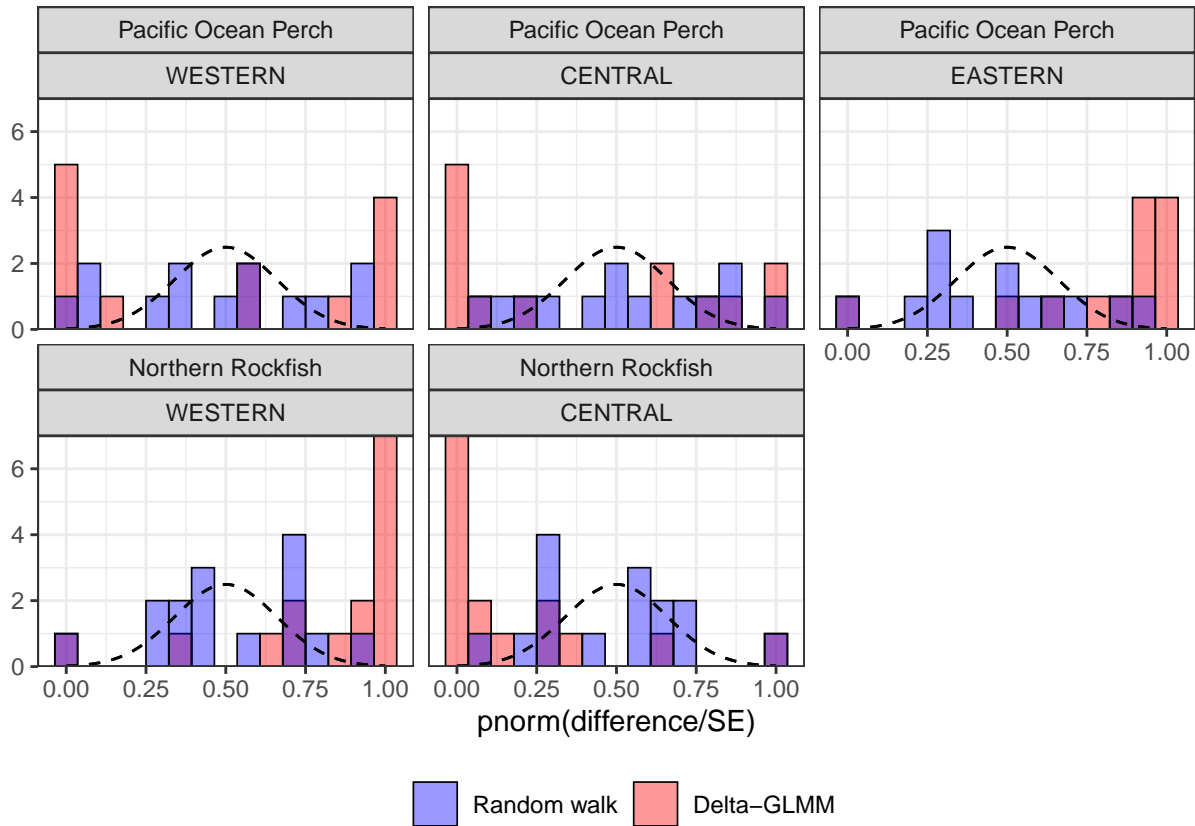


Figure 7: Histogram of the jackknife standard error coverage relative to the difference between the jackknife estimates if the values were normally distributed (using pnorm in R) for random walk (blue shading) and delta-GLMM (red shading) results. A normal curve with a mean of 0.5 and standard deviation of 0.16 is shown by the dashed line to approximate what a normally distributed histogram on a 0 to 1 scale would look like.

514 **Appendix**

515 Table S1. VAST software v3.9.0 and model version 12.0.0 were used to estimate numbers-density
516 and biomass. See Thorson (2019) and <https://github.com/James-Thorson-NOAA/VAST> for details
517 on model settings and inputs. Complete code and model information for this study can be found on
518 the project repository: https://github.com/krmistry/fish_in_space

```
make_settings(Version = "VAST_v12_0_0", n_x = 500, Region = "User",  
  purpose = "index2", ObsModel = c(2, 1), FieldConfig = matrix(c("IID",  
    "IID", "IID", "IID", "IID"), ncol = 2, nrow = 3,  
  dimnames = list(c("Omega", "Epsilon", "Beta"), c("Component_1",  
    "Component_2"))), RhoConfig = c(Beta1 = 2, Beta2 = 2,  
  Epsilon1 = 2, Epsilon2 = 2), strata.limits = data.frame(STRATA = as.factor(c("Western",  
    "Central", "Eastern")), west_border = c(-Inf, -159, -147),  
  east_border = c(-159, -147, Inf)), knot_method = "grid",  
  fine_scale = TRUE, bias.correct = TRUE, use_anisotropy = TRUE)
```

519 Table S2. Definitions of all symbols used in the model and evaluation metrics equations, divided into
520 three sections; parameter and data symbols used in the random walk model equations, parameter and
521 data symbols used in the delta-GLMM model equations, and symbols used in the model evaluation
522 equations.

Symbol	Definition
Random Walk	
x_t	true biomass at time t
$\theta_{\rho,t}$	process variation at time t
σ_p	standard deviation of process error
y_t	survey biomass at time t
$\theta_{o,t}$	observation error at time t
$\sigma_{o,t}$	standard deviation of observation error for time t
Delta-GLMM	
$p_{i,s,t}$	encounter probability of observation i at location s and time t
$n_{i,s,t}$	log-link function for encounter probability with fixed & random effects
$a_{i,s,t}$	offset for area for encounter probability
$\beta_{1,t}$	temporal effect (random or fixed depending on species) for encounter probability
$v_{1,s}$	spatial random effect for encounter probability
$\epsilon_{1,s,t}$	spatio-temporal random effect for encounter probability
R	matrix of the spatial correlations for the entire area given an estimated distance κ
σ_{1v}^2	estimated pointwise variances of spatial variation in $v_{1,s}$
$\sigma_{1\epsilon}^2$	estimated pointwise variances of spatial variation in $\epsilon_{1,s,t}$
$w_{i,s,t}$	log-link function for positive catch with fixed & random effects
$\beta_{2,t}$	temporal random effect for positive catch
$v_{2,s}$	spatial random effect for positive catch
$\epsilon_{2,s,t}$	spatio-temporal random effect for positive catch
σ_{2v}^2	estimated pointwise variances of spatial variation in $v_{2,s}$
$\sigma_{2\epsilon}^2$	estimated pointwise variances of spatial variation in $\epsilon_{2,s,t}$
Model Evaluation	
$b_{c,t}$	estimated biomass in subregion c in year t
B_t	sum of biomass in all subregions in year t
$P_{c,t}$	proportion of total biomass in subregion c in year t
$D_{c,e}$	absolute difference for subregion c in year e (from excluded years)
$P_{r,c,e}$	proportion of model estimated total biomass in subregion c in year e
$P_{d,c,e}$	design-based proportion for subregion c in year e
$CV_{c,e}$	coefficient of variation for subregion c in year e
$SE[P_{r,c,e}]$	standard error of the model estimated proportion of total biomass for subregion c in year e
$SE[b_{c,e}]$	model estimated standard error of the biomass in subregion c in year e
$CV_{c,t}$	CV value for model estimates fit with all data for subregion c and year t

Loading [MathJax]jax/output/HTML-CSS/fonts/TeX/fontdata.js

524 **References**

- 525 Allaire, J., Y. Xie, J. McPherson, J. Luraschi, K. Ushey, A. Atkins, H. Wickham, J. Cheng, W.
526 Chang, and R. Iannone. 2022. Rmarkdown: Dynamic documents for r.
- 527 Brodie, S. J., J. T. Thorson, G. Carroll, E. L. Hazen, S. Bograd, M. A. Haltuch, K. K. Holsman,
528 S. Kotwicki, J. F. Samhuri, E. Willis-Norton, and R. L. Selden. 2020. Trade-offs in covariate
529 selection for species distribution models: A methodological comparison. *Ecography* 43:11–24.
- 530 Ciannelli, L., P. Fauchald, K. S. Chan, V. N. Agostini, and G. E. Dingsør. 2008. Spatial fisheries
531 ecology: Recent progress and future prospects. *Journal of Marine Systems* 71:223–236.
- 532 Costello, C., D. Ovando, T. Clavelle, C. K. Strauss, R. Hilborn, M. C. Melnychuk, T. A. Branch, S.
533 D. Gaines, C. S. Szuwalski, R. B. Cabral, D. N. Rader, and A. Leland. 2016. Global fishery
534 prospects under contrasting management regimes. *Proceedings of the National Academy of*
535 *Sciences* 113:5125–5129.
- 536 Davison, R., M. Stadman, and E. Jongejans. 2019. Stochastic effects contribute to population
537 fitness differences. *Ecological Modelling* 408:108760.
- 538 Fissel, B. 2020. Economic Status of the Groundfish Fisheries Off Alaska:211.
- 539 Fissel, B., A. Abelman, M. Dalton, B. Garber-Yonts, A. Haynie, S. Kasperski, J. Lee, D. Lew,
540 C. Seung, K. Sparks, M. Szymkowiak, and S. Wise. 2020. STOCK ASSESSMENT AND
541 FISHERY EVALUATION REPORT FOR THE GROUND FISH FISHERIES OF THE GULF
542 OF ALASKA AND BERING SEA/ALEUTIAN ISLANDS AREA: ECONOMIC STATUS OF
543 THE GROUND FISH FISHERIES OFF ALASKA, 2020. Page 287. NOAA NMFS Alaska
544 Fisheries Science Center.
- 545 Holsman, K. K., E. L. Hazen, A. Haynie, S. Gourguet, A. Hollowed, S. J. Bograd, J. F. Samhuri,
546 and K. Aydin. 2019. Towards climate resiliency in fisheries management. *ICES Journal of*
547 *Marine Science* 76:1368–1378.
- 548 Hulson, P.-J. F., Chris R. Lunsford, and Darin Jones. 2020. Assessment of the Pacific ocean perch
549 stock in the Gulf of Alaska. *North Pacific Fishery Management Council*:79.
- 550 Levin, S., and C. Goodyear. 1980. Analysis of An Age-structured Fishery Model. *Journal of*
551 *Mathematical Biology* 9:245–274.

552 Lindgren, F., H. Rue, and J. Lindström. 2011. An explicit link between Gaussian fields and Gaussian
553 Markov random fields: The stochastic partial differential equation approach. *Journal of the*
554 *Royal Statistical Society: Series B (Statistical Methodology)* 73:423–498.

555 Methot, R. 2009. *Stock Assessment: Operational Models in Support of Fisheries Management.*
556 Pages 137–165.

557 O’Leary, C. A., J. T. Thorson, J. N. Ianelli, and S. Kotwicki. 2020. Adapting to climate-driven
558 distribution shifts using model-based indices and age composition from multiple surveys in the
559 walleye pollock (*Gadus chalcogrammus*) stock assessment. *Fisheries Oceanography* 29:541–557.

560 Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian
561 models by using integrated nested Laplace approximations. *Journal of the Royal Statistical*
562 *Society: Series B (Statistical Methodology)* 71:319–392.

563 Schnute, J. 1987. A General Fishery Model for a Size-Structured Fish Population. *Canadian Journal*
564 *of Fisheries and Aquatic Sciences* 44:924–940.

565 Stauffer, G. 2004. NOAA Protocols for Groundfish Bottom Trawl Surveys of the Nation’s Fishery
566 Resources. NOAA Technical Memorandum NMFS-SPO-65.

567 Thorson, J. 2017. Three problems with the conventional delta-model for biomass sampling data,
568 and a computationally efficient alternative. *Canadian Journal of Fisheries and Aquatic Sciences*
569 75.

570 Thorson, J. T. 2019. Guidance for decisions using the Vector Autoregressive Spatio-Temporal
571 (VAST) package in stock, ecosystem, habitat and climate assessments. *Fisheries Research*
572 210:143–161.

573 Thorson, J. T., and L. A. K. Barnett. 2017. Comparing estimates of abundance trends and
574 distribution shifts using single- and multispecies models of fishes and biogenic habitat. *ICES*
575 *Journal of Marine Science* 74:1311–1321.

576 Thorson, J. T., C. J. Cunningham, E. Jorgensen, A. Havron, P.-J. F. Hulson, C. C. Monnahan,
577 and P. von Szalay. 2021. The surprising sensitivity of index scale to delta-model assumptions:
578 Recommendations for model-based index standardization. *Fisheries Research* 233:105745.

579 Thorson, J. T., and M. A. Haltuch. 2018. Spatiotemporal analysis of compositional data: Increased
580 precision and improved workflow using model-based inputs to stock assessment. *Canadian*

581 Journal of Fisheries and Aquatic Sciences.

582 Thorson, J. T., A. O. Shelton, E. J. Ward, and H. J. Skaug. 2015. Geostatistical delta-generalized lin-
583 ear mixed models improve precision for estimated abundance indices for West Coast groundfishes.
584 ICES Journal of Marine Science 72:1297–1310.

585 Van Beveren, E., D. E. Duplisea, J. R. Marentette, A. Smith, and M. Castonguay. 2020. An example
586 of how catch uncertainty hinders effective stock management and rebuilding. Fisheries Research
587 224:105473.

588 Williams, B. C., P.-J. F. Hulson, C. R. Lunsford, C. J. Cunningham, and D. H. Hanselman.
589 2020. Assessment of the Northern Rockfish stock in the Gulf of Alaska. North Pacific Fishery
590 Management Council:77.

591 Xie, Y. 2014. Knitr: A comprehensive tool for reproducible research in R. *in* V. Stodden, F.
592 Leisch, and R. D. Peng, editors. Implementing reproducible computational research. Chapman;
593 Hall/CRC.

594 Xie, Y. 2015. Dynamic documents with R and knitr. 2nd edition. Chapman; Hall/CRC, Boca
595 Raton, Florida.

596 Xie, Y. 2021. Knitr: A general-purpose package for dynamic report generation in r.

597 Xie, Y., J. J. Allaire, and G. Grolemond. 2018. R markdown: The definitive guide. Chapman;
598 Hall/CRC, Boca Raton, Florida.

599 Xie, Y., C. Dervieux, and E. Riederer. 2020. R markdown cookbook. Chapman; Hall/CRC, Boca
600 Raton, Florida.

601 Xu, L., B. Li, X. Chen, and Y. Chen. 2019. A comparative study of observation-error estimators
602 and state-space production models in fisheries assessment and management. Fisheries Research
603 219:105322.

604 Ying, Y., Y. Chen, L. Lin, and T. Gao. 2011. Risks of ignoring fish population spatial structure in
605 fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 68:2101–2120.