1 **Comparison of multiple approaches to calculate time-varying biological reference points in**
2 **climate-linked population-dynamics models**

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15   **Abstract**

16   Fisheries managers use biological reference points (BRPs) as targets or limits on fishing

17   and biomass to maintain productive levels of fish stock biomass. There are multiple ways to

18   calculate BRPs when biological parameters are time-varying. Using summer flounder

19   (*Paralichthys dentatus*) as a case study, we investigated time-varying approaches in concert with

20   climate-linked population models to understand the impact of environmentally-driven variability

21   in natural mortality, recruitment, and size-at-age on two commonly-used BRPs ($B_0(t)$ and $F_{35\%}$

22   (t)). We used two approaches to calculate time-varying BRPs: dynamic-BRP and moving-

23   average-BRP. We quantified the variability and uncertainty of different climate dependencies

24   and estimation approaches, attributed BRP variation to variation in life-history processes, and

25   evaluated how using different approaches impacts estimates of stock status. Results indicate that

26   the dynamic BRP approach using the climate-linked natural mortality model produced the least

27   variable reference points compared to others calculated. Summer flounder stock status depended

28   on the estimation approach and climate model used. These results emphasize that understanding

29   climate dependencies is important for summer flounder reference points and perhaps other

30   species, and careful consideration is warranted when considering what time-varying approach to

31   use, ideally based upon simulation studies within a proposed set of management procedures.

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37   **Keywords**: fisheries management, climate, biological reference points, environmental effects,

38   time-varying

Introduction

In fisheries management, an estimate of the fish stock state is compared with a biological reference point (BRP) to define the stock status. The BRP is typically related to a biologically sustainable population size. This comparison is critical to determine if a stock is overfished and whether any changes are needed in current management to meet targets (Gabriel and Mace 1999, Quinn and Deriso 1999, Collie and Gislason 2001, Hilborn 2002, Haltuch *et al.* 2008). Harvest control rules are guidelines that determine how much fishing can occur based on the current state of the system relative to target and/or limit reference points for the stock size and catch/fishing effort (Deroba and Bence 2008). Harvest control rules attempt to balance biological, economic, and social sustainability and often use BRPs to define the limit and target for catch. The goal of a BRP-based management framework is to regulate fishing by setting a quota such as a fishing mortality rate or biomass threshold that is based on BRPs. For example, the fishing quota produced using the spawning potential ratio (SPR), a common metric used in fisheries management, is based on a preset fixed ratio of fished and unfished spawning biomass per recruit (SBPR) (Gabriel *et al.* 1989, Goodyear 1993, Williams and Shertzer 2003).

The BRPs are based on parameters that reflect the long-term productivity of the fish stock, such as growth, recruitment, and mortality (Williams and Shertzer 2003, Maunder 2012), all of which can vary in response to a variety of factors. Productivity can vary over time for many different reasons, such as changes in the environment, available food, predation mortality, or fishing pressure, and this directly affects the management process (Jackson *et al.* 2001, Pitchford *et al.* 2005, Vert-pre *et al.* 2013, Nye *et al.* 2014, Pershing *et al.* 2015, Koenigstein *et al.* 2016, Collie *et al.* 2017, Stock *et al.* 2017, Barrow *et al.* 2018). Climate can impact productivity directly through physiological effects in response to temperature conditions and a change in the allocation of energy between growth and reproduction (Buckley *et al.* 2004, Baudron *et al.* 2011, 2014). Climate can also impact productivity indirectly through predator-prey interactions (such as a change in community composition and overlap of a predator or prey), fish behavior, or recruitment via reproductive potential, timing of spawning or migration, and larval growth (Blanchard *et al.* 2005, Laurel *et al.* 2007). Many studies have found that fish population fluctuations are associated with large-scale climate variability (Lehodey *et al.* 2006, Brander 2007, Brander 2010, Holsman *et al.* 2012, Barange *et al.* 2014, Free *et al.* 2019). Not

70   accounting for productivity changes may lead to errors in biological reference point estimation

71   (Whitten *et al.* 2013, Audzijonyte *et al.* 2016, Karp *et al.* 2019). One approach to deal with

72   temporal variability is to calculate BRPs using the average stock dynamics over the most recent

73   3-5 years or across the entire period being modeled.

74   More recently, as part of the move to include a broader set of considerations in stock

75   assessments, fisheries scientists have attempted to incorporate environmental effects into

76   fisheries models (Hare *et al.* 2016, Tommasi *et al.* 2017b). There are uncertainties regarding the

77   fish stock's dynamics and interaction with its environment (Hilborn and Walters 1992, Quinn

78   and Deriso 1999, Maunder 2012). Given that environmental variability changes vital rates such

79   as recruitment and natural mortality and progress has been made to incorporate these processes

80   explicitly in stock assessments, understanding BRPs in the context of climate is crucial (Mantua

81   and Hare 2002, A'mar *et al.* 2009, Thorson *et al.* 2015, O'Leary *et al.* 2018). Demographic

82   changes due to variation in fish vital rates can change BRPs and thus, stock status and catch

83   quotas. The magnitude of the effect of these changes on BRPs depends on the BRP used (Gerber

84   and Heppell 2004, Frisk *et al.* 2005, Thorson *et al.* 2015). Miller *et al.* (2018) found that

85   incorporating environmental indices into a stock-assessment model not only influenced Georges

86   Bank Atlantic cod (*Gadus morhua*) demographic estimates and BRPs but also increased the

87   uncertainty in BRP estimates. Therefore, tailoring BRPs to climate state is a particularly

88   important management strategy if future population conditions differ from past conditions due to

89   a changing climate and a consequent regime shift; that is, an abrupt change within the population

90   (A'mar *et al.* 2009, Punt *et al.* 2016). If past stock conditions are used to estimate future stock,

91   these catch targets are often unsustainable (Haltuch *et al.* 2009, Punt *et al.* 2016). If the influence

92   of climate on a fish stock is understood and successfully modeled, there is still a choice on how

93   to incorporate these temporal dynamics into BRP calculations that likely will influence the BRP

94   estimate (Berger 2018).

95   Two main approaches can be used to incorporate temporal dynamics (and consequently

96   climate influence) into BRP calculation; (1) dynamic-BRPs and (2) moving-average-BRPs. The

97   dynamic-BRP is a generalization of the dynamic-B_0 from MacCall *et al.* (1985) that calculates

98   the SBPR following each cohort through time at a set fishing pressure (F*) given estimated

99   parameters for stock productivity from an unfished population (MacCall *et al.* 1985, Haltuch *et*

100 *al.* 2009, Punt and Donovan 2007). The dynamic approach is referred to as 'dynamic' because it

101   generalizes 'dynamic-B_0', i.e., where it projects dynamics from *t-1* to *t* in the absence of fishing

102   (to calculate biomass targets from B_0) or with different fishing mortality rates (to calculate

103   exploitation targets from SPR). The moving-average-BRP is an equilibrium approach that

104   assumes natural mortality, growth, and other biological processes in year *t* (or a defined time-

105   interval) are held constant (at their value in a single year or average across years) to calculate

106   stock productivity (Cordue 2012, Punt and Donovan 2007).

107   More informed management decisions can be achieved by understanding the properties

108   and assumptions that led to the BRPs used in management, and whether these summaries of

109   temporal and environmental dynamics are appropriate for stock management (Walters and Parma

110   1996, McAllister *et al.* 1999, Punt and Donovan 2007, Kolody *et al.* 2008, Kurota *et al.* 2010,

111   Punt *et al.* 2016). If changes in fish stock productivity are missed due to an inaccurate

112   relationship between a stock and environment or summarizing a stock's dynamics in a way that

113   smooths over important dynamics, effective BRP-based management is compromised. Therefore,

114   a comparison of different time-varying approaches to BRP estimation with different forms of

115   climate-dependencies in those calculations will help illuminate how variability and climate

116   influence BRP-based management.

117   The purpose of this paper was twofold, (A) to examine the effects of climate dependency

118   on BRP variability and uncertainty used in harvest control rules, and (B) to determine how

119   sensitive estimates of BRPs are to the choice of "dynamic" or "moving-average" BRP

120   approaches. We use summer flounder, a demersal flatfish found in the Northwest Atlantic, as an

121   empirical case study to investigate BRPs. To evaluate the implications of both climate

122   assumptions and estimation approaches on the BRP value output, our objectives were to (1)

123   quantify the variability over time of climate-dependent vs. climate-independent BRPs

124   (henceforth "variability"); (2) quantify the standard error for different BRPs and approaches

125   (henceforth "uncertainty"); (3) determine whether moving-average- or dynamic-BRPs are more

126   variable and uncertain over time; (4) attribute trends and variation in BRPs to variation in

127   mortality, recruitment, and growth processes; and (5) evaluate how different methods impact

128   estimates of stock status for summer flounder (*Paralichthys dentatus*). Given the importance of

129   the BRPs in the management framework and the likely influence of both types of temporal

130   variability and method of incorporation, we sought to demonstrate the implications of both the

131   estimation approach and climate dependency on the reference BRP value.

132

Methods

134   We use two different temporally-varying methods to provide information regarding the

135   impact of BRP calculation choices on management reference points through direct comparison of

136   BRP uncertainty and temporal variability differences. Here, we aim to fill the gap in BRP

137   documentation and methods development by comparing the differences in BRPs calculated from

138   different climate relationships with biological parameters and different approaches to accounting

139   for temporal dynamics.

140

Population models with climate dependencies

142   Posterior distributions for parameters used in BRP calculations were drawn from

143   previously constructed hierarchical population models used to understand changes in past

144   summer flounder abundance (Figs. 1-2, O'Leary *et al.* 2018). Summer flounder is a data-rich

145   stock where fishing pressure and environmental variability were shown to impact population

146   dynamics. Moving-average- and dynamic-BRPs were compared in three population models that

147   differed in their link to the environment: a climate-dependent natural mortality relationship

148   (CM); a climate-dependent recruitment relationship (CR); and no relationship with

149   environmental conditions (CI) (O'Leary *et al*. 2018). Here, the climate covariate or T_t represents

150   the Gulf Stream Index, the index used to describe climate conditions in the Northwest Atlantic,

151   which is available for every modeled year *t*. The natural mortality and recruitment estimates for

152   each model type can be seen in Fig. 2. These relationships were established and tested in

153   O'Leary *et al.* (2018) that found overall the Gulf Stream Index provided information to improve

154   the estimation of natural mortality and subsequently fishing mortality. The Gulf Stream Index

155   represents the position of the north wall of the Gulf Stream and provides an integrative

156   representation of oceanographic conditions of the Northeast US shelf. The Gulf Stream Index

157   was used to represent the emergent properties of the local environment to which the organisms

158   are responding. We did not consider models with multiple types of climate effects so that we

159   could first determine the impact of the mechanism by which   climate affected population

160   dynamics in isolation. The models considered age-specific population processes and included

161   both process and observation error. We used two data sources from 1982 – 2015 in the

162   population models: 1) fisheries-independent annual bottom trawl surveys by the Northeast

163   Fisheries Science Center (NEFSC; Azarovitz 1981, Clark *et al.* 1997) and 2) fisheries-dependent

164   commercial and recreational landings of summer flounder (Burns *et al.* 1983) from the NEFSC

165   fisheries database. Parameters of Bayesian hierarchical models were estimated from empirical

166   data using Just Another Gibbs Sampler (JAGS; Plummer 2003) integrated through R version

167   3.2.4 (R Core Team 2017) using R package 'R2Jags' (Su and Yajima 2012). As a group, we

168   refer to these models described in the following sections as estimation models.

169

Including the effects of climate on population dynamics

171   The three population models followed a general structure described below as a simpler

172   version of the summer flounder stock-assessment model, with variations in either the natural

173   mortality or recruitment equation. Summer flounder abundance ($N_{a,t}$) was estimated across time

174   (*t*) by age (*a*) from age-at-recruitment (age 0, *a* = 0) to age 7 + (any fish age 7 or older is treated

175   as a part of a single "plus group") (Eqn. 1 a, b), where initial abundance is defined by

176   recruitment R_t for year t:

177    $$N_{a,t} = \begin{cases} R_t & a = 0 \\ e^{-Z_{a-1,t-1}}N_{a-1,t-1} & 1 \leq a \leq 6 \\ e^{-Z_{a-1,t-1}}N_{a-1,t-1,} + e^{-Z_{a,t-1}}N_{a,t-1} & a \geq 7 \end{cases} \qquad \textbf{(1a)}$$

178   where survival was specified as $s_{a,t} = e^{-Z_{a,t}}$, and the total mortality $Z_{a,t}$ consisted of natural

179   mortality $M_{a,t}$ and fishing mortality $F_{a,t}$: $Z_{a,t} = M_{a,t} + F_{a,t}$. Recruitment was estimated by

180   predicting log-recruitment given spawning biomass and a multiplicative lognormal residual

181   variability. In this study, *log()* is used to indicate the natural log. Log-recruitment $\log(R_t)$

182   (defined as abundance at *a* = 0), was parameterized as recruitment deviations:

183    $\log(R_t) = f(SB_t) + \varepsilon_t$ **(1b)**

184   where $f(SB_t)$ is the Beverton-Holt function predicting log-recruitment as a function of spawning

185   stock biomass,

186    $$f(SB_t) = \begin{cases} \log\left(\frac{SB_{t-1}}{\beta + \alpha SB_{t-1}}\right) & \textit{if using CI or CM model} \\ \log\left(\frac{SB_{t-1}}{\beta + \alpha SB_{t-1}}e^{cT}\right) & \textit{if using CR model} \end{cases} \qquad \textbf{(2)}$$

187   and recruitment deviations are the normally distributed variable $\varepsilon_t \sim Normal(-\frac{\sigma_r^2}{2}, \sigma_r^2)$ (Eqn. 1b;

188   Terceiro 2015, 2016, Methot and Taylor 2011). Climate-covariate effects (*c*) on recruitment were

189   allowed in the general model. The recruitment-environment relationship used in the CR model is

190 controlling recruitment (as opposed to limiting or masking), where climate is expected to

191 influence recruitment via the larval/young fish mortality rates (Iles and Beverton 1998, O'Leary

192 *et al.* 2018), while in the CI and CM model it was the standard Beverton-Holt form. The

193 recruitment estimates for each model type can be seen in Fig. 2.

194 The R package 'Fish Life' was used to provide a starting point for an informative prior

195 for α to the nearest integer (log-normally distributed with a log-mean of 3 and a log-standard

196 deviation of 1; Thorson *et al.* 2017). Fish Life was also used to create an informative prior for the

197 standard deviation of recruitment deviations, σ_r^2 (bounded between 0.1 and 0.9) to be used in the

198 estimation of the variance ε_t (Thorson *et al.* 2017). Log-abundance, $\log(N_{a,1})$, for each age a in

199 the first modeled year was assigned a uniform prior distribution with realistic biological bounds

200 selected such that the prior distribution did not qualitatively affect model results. Spawning stock

201 biomass (SB_t) was dependent upon the abundance at age a at time t ($N_{a,t}$), weight-at-age a at

202 time t ($w_{a,t}$; $Fig.\,1$), maturity at age a (m_a) up to the final age class a_{max}

203 $SB_t = \frac{1}{2}\sum_{a=1}^{a_{max}} w_{a,t} m_a N_{a,t}$ **(3)**

204 where we specify that females represent 50% of total abundance.

205 For all three estimation models, we modeled natural mortality ($M_{a,t}$) as a time- and age-

206 varying process, with values drawn from a lognormal distribution with log-mean ($V_{a,t}$;

207 hyperparameter for natural mortality) and variance (σ_M^2)

208 $\log(M_{a,t}) \sim Normal(V_{m,a,t}, \sigma_M^2)$, **(4)**

209 where the specification of $V_{m,a,t}$ differs among models m.

210 In the climate-dependent mortality model (CM), the log-mean of natural mortality

211 ($V_{m,a,t}$) followed a quadratic function of climate, while it was constant for CI and CR models:

212 $V_{m,a,t} = \begin{cases} x_0 & \text{if using CI or CR models} \\ x_0 + x_1 T_t + x_2 T_t^2 & \text{if using CM model} \end{cases}$. **(5)**

213 We incorporated the estimate of natural mortality $M_{a,t}$ for each age and year (Eqn. 4 – 5) into the

214 survival equation. The log-quadratic relationship of the Gulf Stream Index -natural mortality

215 relationship is suggested to be related to both preferred warmer temperatures that occur at high

216 Gulf Stream Index when the north wall of the Gulf Stream is pushed further north, and changes

217 in available habitat (that consequently impacts mobility, predator and prey densities, and

218   ontogenetic migration) (O'Leary *et al.* 2018). For full methods, the remaining equations, prior

219   distributions, and equation definitions see O'Leary *et al.* (2018).

220

Biological Reference Point Calculation

222   We calculated twelve time-series of BRPs from 1990 - 2015, formed as the factorial cross

223   of three estimation models (explained previously) and two approaches to estimating BRPs

224   (dynamic and moving-average) for two BRPs (a fishing-mortality and a spawning-biomass BRP)

225   that utilize the spawning potential ratio or SPR, also defined below. The four paired estimation

226   approaches and BRP calculations were dynamic-$B_0(t)$, dynamic- $F_{35\%}(t)$, moving-average-

227     $B_0(t)$, and moving-average- $F_{35\%}(t)$. BRP calculations begin in 1990 because the dynamic-BRP

228   calculations require information on population processes for the lifespan of summer flounder, in

229   this case 8 years for the last recorded age class plus group (i.e., initial year of data available

230   (1982) + full range of age classes in the model (8 years) = 1990. We calculated each time series

231   as a posterior predictive distribution given the posterior distribution for parameters in the CI, CR,

232   and CR models. For consistency with the NOAA stock assessment of summer flounder (Terceiro

233   2016), we use the SPR-based BRP ($F_{35\%}(t)$) as a proxy for F_{MSY} (Table 1). Previous research

234   defined 0.35 as a sufficient ratio to maintain SBPR levels that meet management targets for New

235   England groundfish (Clark 1991), although Clark (1993) noted that in the presence of randomly

236   variable recruitment 0.40 was a better ratio than 0.35.

237   For each BRP, we used 2,850 Markov Chain Monte Carlo samples (*r*) from the posterior

238   distribution for parameters in each estimation model. For each posterior sample, we projected

239   population dynamics for 201 levels of fishing (F^*) ranging from 0 to 2 in increments of 0.01,

240   resulting in 572,850 total projections. The following sections detail the calculations used by for

241   dynamic-BRP and moving-average-BRP approaches for the reference points $F_{35\%}(t)$ and $B_0(t)$.

242

BRP Calculation Algorithm

244   The main difference between the dynamic- and moving-average- $F_{35\%}(t)$ and $B_0(t)$ are

245   the method of incorporation of temporal variability. The dynamic approach incorporated the

246   varying vital rates of a cohort through time to calculate productivity given estimated parameters

247   for stock productivity from a dynamic B_0 estimated population. In the dynamic-BRP approach,

248   the population was projected using values in year *t-1* for each cohort. Therefore, the population

249   dynamics reflect estimates of demographic parameters (recruitment, natural mortality, growth,

250   and maturity) for preceding years. The dynamic approach is referred to as 'dynamic' because it

251   generalizes 'dynamic-B_0', i.e., where it projects dynamics from *t-1* to *t* in the absence of fishing

252   (to calculate biomass targets from B_0) or with different fishing mortality rates (to calculate

253   exploitation targets from SPR). The moving-average approach is calculated assuming

254   equilibrium conditions given a set of environmental conditions and demographic parameters in a

255   given year (or their average over a window of years) at a specified level of fishing over the entire

256   time-period of the population.

257   To calculate dynamic-$B_0(t)$, dynamic-$F_{35\%}(t)$, moving-average-$B_0(t)$, and moving-

258   average-$F_{35\%}(t)$ we used the following general steps: (1) calculate unfished spawning biomass

259   per recruit and spawning potential ratio; and (2) calculate total numbers and unfished biomass,

260   for 201 levels of F^* ranging from 0 to 2 in increments of 0.01. Calculations used a sample $\boldsymbol{\theta}_r$ for

261   natural mortality, recruitment deviations, initial age-structure, selectivity, and initial numbers-at-

262   age from an estimation model posterior distribution *r*. Full algorithms with equations for each

263   BRP calculation can be found in Supplementary Materials 1.

264   ***Evaluation of Estimation Approaches***

265   We calculated the mean, uncertainty, and variability (i.e., the temporal coefficient of

266   variation due to biological variation) of $F_{35\%}(t)$ and $B_0(t)$ over the entire period to address the

267   first three objectives: (1) quantify the variability over time of climate-dependent vs. climate-

268   independent BRPs over a 26-year period; (2) quantify the standard error for different BRPs and

269   approaches; and (3) determine whether moving-average- or dynamic-BRPs are more variable

270   and uncertain over time. We calculated uncertainty as the mean of the CVs across *L* samples of

271   the posterior x_r for *Y* years, where $CV_y = \dfrac{\sqrt{\frac{1}{L}\sum_{r=1}^{L}(x_r-\mu)^2}}{\frac{\sum_{r=1}^{L}x_r}{L}}$ and average $uncertainty = \dfrac{\sum_{y=1}^{Y}CV_y}{Y}$.

272   Temporal variability was calculated as the CVs across a total of *Y* years for a total of *L* posterior

273   samples followed by a mean across samples. Here, $CV_r = \dfrac{\sqrt{\frac{1}{Y}\sum_{y=1}^{Y}(x_y-\mu)^2}}{\frac{\sum_{y=1}^{Y}x_y}{Y}}$ and temporal

274    $variability = \dfrac{\sum_{r=1}^{L}CV_r}{L}$.

275   To address objective (4) to attribute trends and variation in BRPs to variation in
276   mortality, recruitment, and growth processes, we tested three separate model fits: (1) natural
277   mortality varied with all other BRP inputs fixed at their averages, (2) weight-at-age (i.e., growth)
278   varied with all other BRP inputs fixed at their averages, and (3) recruitment varied with all other
279   B_0 inputs fixed at their averages (Miller *et al.* 2018). Each scenario describes the biological
280   process that varied while holding all other biological parameters at their average conditions. In
281   model fits (2) and (3) where natural mortality was constant, it was fixed at the average over time
282   for each age. To address objective (5) to evaluate how different methods impact estimates of
283   stock status for summer flounder, we compared the estimation model fishing rate and spawning
284   stock biomass to estimated moving-average and dynamic $F_{35\%}(t)$ and $B_{35\%}(t)$, or 35% of
285    $B_0(t)$, to determine if the stock was overfished or if overfishing was occurring. We determined
286   'overfished' and 'overfishing' status for summer flounder for each BRP estimation approach and
287   climate-model. Overfishing here is defined as when the current fishing rate is higher than the
288   BRP fishing value. Overfished is defined as when the stock is unable to maintain biomass levels
289   at or above $B_{35\%}(t)$. This is different than the biomass reference point used in the stock
290   assessment for summer flounder, where overfishing is calculated by projection method using the
291   fishing rate at $F_{35\%}$ and average recruitment (Terceiro 2016).
292
293   **Results**
294
295   ***Objective 1: How variable are climate-linked BRPs?***

296   Overall, the temporal variability in $F_{35\%}(t)$ and B_0 was greater for the climate-dependent
297   recruitment (CR) and climate-independent (CI) models than the climate-dependent natural
298   mortality (CM) model for both estimation approaches (Fig. 3, Table 2). This difference in
299   variability indicated that the CM model provided the most stable biological reference points.
300   Additionally, the mean $F_{35\%}(t)$ was lowest for the CM model, indicating that the CM model
301   estimated the most restrictive fishing mortality threshold.
302
303   ***Objective 2: How uncertain are climate-linked BRPS?***

304   Overall, the uncertainty (i.e., CV for the posterior distribution) in both the $F_{35\%}(t)$ and

305    $B_0(t)$ was smaller for the CM model than all other models (Fig. 3, Table 2). This likely occurs

306   because the CM model has a different posterior distribution than the other two models, where the

307   CM model posterior explains more of the population variance (Fig. 2).

308

309   ***Objective 3: Are moving-average-BRPs or dynamic-BRPs more uncertain and variable over***

310   ***time?***

311   The temporal variability in $F_{35\%}(t)$ and $B_0(t)$ was greater for the moving-average-BRP

312   approach than the dynamic-BRP approach for all tested models (Fig. 3, Table 2). These results

313   suggest that tracking individual cohorts (i.e., dynamic-BRP approach) results in less variable

314   fishing and biomass reference points than if the population achieves equilibrium given average

315   demographic rates over a one-year window (i.e., moving-average-BRP approach) because the

316   dynamic-BRP approach is smoothing across cohorts in a given year.

317   Variability in the moving-average-BRP approach also depends upon whether calculations

318   are based on conditions in a single year, 3-year, or 5-year window. As the window to calculate

319   the $F_{35\%}(t)$ increased to 3- and 5-years (both with t as the center and terminal year), variability

320   using the moving-average approach decreased relative to the one-year window (see

321   Supplementary Materials 2). Overall, the moving-average approach $F_{35\%}(t)$ was more variable

322   than the dynamic approach $F_{35\%}(t)$ for all windows (except for the 5-year window with t as the

323   terminal year for the CM model). As the window to calculate $B_0(t)$ increased to 3- and 5-years

324   (with t as the center and terminal year), the moving-average approach variability decreased again

325   relative to the one-year window. Overall, the moving-average approach $B_0(t)$ was more variable

326   than the dynamic approach for the 1- and 3-year windows, and less variable than the dynamic

327   approach for the 5-year window. See Supplementary Materials 2 for the full results for the

328   moving-average approach using 3- and 5-year window averages with t as the center year and t as

329   the terminal year.

330   The uncertainty in the $F_{35\%}(t)$ estimates (i.e., the coefficient of variation of the posterior

331   distribution) was lower in the dynamic-BRP approach than the moving-average-BRP approach

332   (Table 2). The uncertainty in the $B_0(t)$ estimates was also lower in the dynamic-BRP approach

333   than the moving-average-BRP approach (Table 2).

334   The overall temporal trend for $F_{35\%}(t)$ was different between the moving-average and
335   dynamic approach results (Fig. 3). Both the moving-average- and dynamic-$F_{35\%}(t)$ decreased
336   over time for the CR and CI models, and remained relatively constant for the CM model. In the
337   final 5 years (2011 – 2015), the moving-average- $F_{35\%}(t)$ increased whereas the dynamic- $F_{35\%}$
338   (t) continued to decline for the CR and CI models (Fig. 3). The CM model $F_{35\%}(t)$ continued to
339   remain relatively constant over time using both the moving-average-BRP and dynamic-BRP
340   approaches.

341

342   *Objective 4: Attributing variation in BRPs to changes in natural mortality, recruitment, or*
343   *weight-at-age*

344   We explored the impact of each of the three time-varying biological processes in
345   isolation on BRP estimation to determine the causes of observed variation in BRPs: (1) varying
346   weight-at-age, (2) varying natural mortality, and (3) varying recruitment. We found that variation
347   in natural mortality was the largest driver of temporal variation in summer flounder $F_{35\%}(t)$,
348   followed by changes in weight-at-age. For the CR and CI models, we note that temporal
349   variation in estimated natural mortality drives the large decrease in $B_0(t)$ from 2011-2015 in
350   moving-average approach, and therefore drives an associated increase in $F_{35\%}(t)$ for those two
351   models. Variation in natural mortality was the largest driver of temporal variation in summer
352   flounder $B_0(t)$ for the moving-average approach. However, recruitment was the largest driver of
353   variation in summer flounder $B_0(t)$ for the dynamic approach. This suggests that the
354   contribution of temporal variation in natural mortality and recruitment to the BRP variability is
355   dependent on the estimation approach (Fig. 4; Table 3). Figs. 1 – 2 show the time-varying
356   parameters for each of the three estimation models.

357

358   *Objective 5: How do these decisions affect estimates of stock status?*

359   To determine the "overfishing" (i.e., $\frac{F(t)}{F35\%\,(t)} > 1$) and "overfished" (i. e. $\frac{SB(t)}{B_{35\%}(t)} < 1$)
360   status, we calculated the ratio of fishing mortality to $F_{35\%}(t)$ and the spawning stock biomass to
361   35% of $B_0(t)$ (typically called $B_{35\%}(t)$), for both BRP methods for each year. Stock status was
362   highly dependent on the climate model and estimation approach. In the moving-average

363   approach, the stock was classified as overfished up to 2000 (or 2002 in the case of the CM

364   model; Fig. 5). From 2000 up to 2013 (or 2002 – 2005 and 2011 in the case of the CM model),

365   the stock classified as not overfished based upon the moving-average approach BRPs. In the

366   final 2-3 years, the moving-average-BRP estimated the stock as overfished (Fig. 5). In the

367   dynamic approach, the stock was classified as overfished up until 1997 for the recruitment (CR)

368   and natural mortality (CM) models, and up to 1996 for the independent (CI) model (Fig. 5).

369   From that year onward, the stock was classified as not overfished for all models up until the final

370   year 2015 based upon the dynamic approach BRPs. The exception to this was in 2010 for the

371   CM model, where the stock drops back down to overfished. Overfishing was occurring on the

372   summer flounder stock throughout the entire time period based upon BRP calculations from both

373   the moving-average and dynamic approach (Fig. 5), except for in years 1993 and 2002 for the

374   recruitment (CR) and independent (CI) models.

375   For some years (e.g., 1993, 2002), classification as "overfished" (or not) depended on the

376   estimation approach and climate models used. However, it is worth noting how similar the

377   overfishing status is between the two approaches for a given model. As well, the moving-average

378   approach resulted in an overfished stock status for a slightly longer duration. From the

379   management perspective, these small differences can be important because each stock status

380   enacts a different series of management actions. As well, the outcome is affected by any

381   management actions that occurred during this period. All BRP approaches and estimation

382   models classified the stock as overfished with overfishing during early years, with a transition to

383   not overfished with overfishing in later years. The largest difference in stock status between the

384   two estimation approaches is in the final 6 years for the biomass reference, particularly for the

385   independent (CI) and recruitment (CR) models (Fig. 5).

386

387   **Discussion**

388   In this case study using summer flounder, both the mechanism of climate-dependency in

389   the underlying empirical model and the temporal-variability used to calculate biological

390   reference points (BRPs) altered BRP uncertainty, variability, and thus stock status. Specifically,

391   the dynamic-BRP and climate-natural mortality-linked model (CM) estimated lower fishing rates

392   and BRPs for a one-year window than the other models and BRPs tested. BRP variability

393   stemmed principally from varying natural mortality regardless of the estimation approach and

394   underlying climate-dependency model. It is worth noting that O'Leary *et al.* (2018)

395   demonstrated that the climate-natural mortality model (CM) was the best-fitting model to capture

396   past summer flounder abundances. However, because the underlying model used to calculate

397   BRPs can always be incorrectly specified, a more stable or restrictive BRP does not always

398   equate to a 'better' reference point. The climate-dependencies represented here demonstrate how

399   variable fish stock dynamics can be and how the overfishing determination depends on these

400   defined relationships. Previously developed models with time-varying vital rates used to estimate

401   BRPs highlight the importance of correctly identifying climate-dependencies when determining

402   stock status, the large variability in BRP estimates that can result from using climate-dependent

403   models, and the differences in BRP uncertainty depending on the time-varying properties used

404   (i.e., current versus a 3-5 year average).

405   Mangel *et al.* (2013) discuss the false sense of precision that arises from using point

406   estimates or posterior samples when using a two-parameter stock-recruit relationship or fixed

407   natural mortality. Similarly, we suggest that basing reference points on fixed values of life-

408   history parameters will often convey a false sense of precision, given that all populations have

409   some degree of time-varying growth, mortality, maturity, or other processes. Time-varying BRPs

410   inherently have much more variability, may be more difficult to understand, and be difficult for

411   managers to use. We suggest developing time-varying BRPs more generally and comparing them

412   to "static" BRPs to understand this uncertainty hidden by decisions to use fixed natural mortality.

413   Empirical analyses, such as the one presented here, will help managers evaluate risks and

414   priorities through understanding which changing vital rates impact scientific advice to

415   management the most (Karp *et al.* 2019).

416   In this study, time-varying natural mortality resulted in the greatest variability in BRPs in

417   both the climate-recruitment and climate-independent models. The climate-dependent natural

418   mortality (CM) model estimated lower, less variable, and more precise natural mortality

419   parameter estimates than the climate-dependent recruitment (CR) and climate-independent (CI)

420   models. This is likely due to the incorporation of the relationship between natural mortality and

421   the Gulf Stream Index. Additionally, natural mortality decreased slightly in the climate-natural

422   mortality model as the Gulf Stream deviated from average conditions. As natural mortality

423   decreased, peak SBPR at $F_{35\%}(t)$ decreased and occurred at older ages in the climate-natural

424   mortality model. The reduction of peak SBPR, in turn, reduced the BRP value and its associated

425   uncertainty while also providing less variable mean BRPs over time. These changes in

426   productivity are consistent with the theoretical rationale that if natural mortality decreases and all

427   else remains the same, the vital rates describe a longer-lived fish species with productivity

428   spanning over a longer time frame (i.e., the fecundity over the fish's lifetime is greater).

429   Therefore, because of the large influence that time-varying natural mortality has on per recruit

430   BRPs, strong empirical evidence is needed to support the use of a time-varying natural mortality

431   in BRP calculations (Legault and Palmer 2015).

432   The choice to include climate-dependency or temporally varying vital rates in BRP

433   calculations based on empirical evidence can have implications for stock status. Depending on a

434   stock's vulnerability to changing ocean conditions, these differences in BRPs due to assumed

435   temporal dynamics will need to be considered in any risk assessment evaluation. The methods

436   herein provide a tool for scientists and managers to consider when preparing their fishery for

437   both near-term and long-term management under shifting oceanographic conditions. In the case

438   of summer flounder, the temporal variability in $F_{35\%}(t)$ and $B_0(t)$ was greater for the moving-

439   average-BRP approach than the dynamic-BRP approach for all climate models using a 1-year

440   window. The assumed temporal dynamics for each cohort can potentially explain the greater

441   variability in $F_{35\%}(t)$ and $B_0(t)$ in the one-year window moving-average-BRP approach

442   compared to the dynamic-BRP approach. The dynamic-BRP approach tracks cohorts and uses

443   the time-varying natural mortality from that year and all previous years to calculate $F_{35\%}(t)$ and

444    $B_0(t)$. The dynamic approach reflected the productivity at each age in the cohort's lifespan using

445   the natural mortality specific to that age giving each cohort a different productivity history.

446   Because we calculated each cohort with age-specific natural mortality values, the productivity

447   between cohorts within a year was more consistent because it represents a blend of productivities

448   up to that year. The moving-average-BRP approach, on the other hand, was an equilibrium

449   approach (i.e., assuming that environmental conditions continue for indefinitely long period such

450   that the population achieves population equilibrium). The natural mortality was conditioned from

451   a 1-year period (i.e., ignores the cohort history) and assumed equal to that value for the previous

452   years of that cohort's lifespan. Therefore, the productivity of each cohort in any year is

453   calculated in the moving-average approach assuming its productivity at that point in time. This is

454   likely why the moving-average BRP from year to year is more variable than the dynamic BRP.

455   Trends in both BRPs were primarily attributed to natural mortality (Table 2; varying

456   natural mortality scenario). This finding supports the suggestions of Brodziak *et al.* (2011) and

457   Thorson *et al.* (2015) that identifying changes in natural mortality should be a priority when

458   expanding stock assessments to including time-varying biological processes because of their

459   large influence over spawning biomass and catch management targets. As well, in the varying

460   natural mortality scenario, the variability in both BRPs were lowest in the climate-natural

461   mortality model. This suggests that including an environmental index as a covariate in the

462   estimation of natural mortality successfully constrained variation in natural mortality in the

463   climate-natural mortality model, whereas natural mortality was estimated as an unconstrained

464   random process in climate-dependent recruitment and independent models. Different methods of

465   incorporating temporal variability and climate effects into the fish's population dynamics

466   influence the uncertainty and variability of BRPs. Therefore, careful consideration is warranted

467   when considering which approach to use and how to incorporate climate effects, ideally based

468   upon management strategy evaluation within a proposed set of management procedures (Karp *et*

469   *al.* 2019).

470   The variability in the moving-average approach BRPs was highly dependent not only on

471   natural mortality values, but also on the length of window used to calculate the moving-average-

472   BRP. The assumed dynamics for each cohort over the BRP calculation period likely explain the

473   different temporal variability in BRPs for each estimation approach. For the one-year window,

474   this may be due to the large increase in natural mortality in the final year of the models where

475   climate and natural mortality are not linked. The large increase in time-varying natural mortality

476   in the final year is due to insufficient information in the parameterization of these models relative

477   to the climate-linked natural mortality- models. This characteristic is not present in the summer

478   flounder stock assessment due to a different parameterization of natural mortality.

479   We can implement these developed approaches for an MSY reference point where the

480   stock more closely follows a stock-recruit relationship. The models used in this study do contain

481   a stock-recruit relationship. However, the stock-recruit relationship for summer flounder is weak

482   and uncertain (Terceiro 2016). The interpretation of an MSY-based reference point, therefore,

483   was not meaningful or dependable, hence the use of $F_{35\%}(t)$ both here and in the stock

484   assessment (Maunder 2012). Natural mortality has a considerable influence on F_{MSY} similar to

485   $F_{35\%}(t)$ as demonstrated here, and so would be interesting to look at for other stocks (Maunder

486   2012).

487   In the 2019 summer flounder stock assessment, the stock was determined not overfished

488   and no overfishing was occurring. As well, based on the BRPs calculated here, there was no

489   overfishing of the summer flounder stock despite differences in BRP uncertainty and variability

490   in this study. Some of the calculated BRPs in this paper did categorize summer flounder as

491   overfished in recent years, which can potentially trigger a rebuilding plan if the fishing mortality

492   is not low enough to allow the stock to be projected to be rebuilt in sufficient time. However, the

493   purpose of this study was not to present the 'correct' BRP values or BRP values for

494   management, but rather to present the consequences of considering multiple model productivity

495   estimates and BRP calculation approaches within the same stock. The models used to explore the

496   consequences of the estimation model and estimation approach are simpler than typical stock

497   assessment models so that we could incorporate time-varying natural mortality and other time-

498   varying processes. For instance, fleets in this study combine landings and discards, likely

499   influencing the magnitude of BRP values. As well, the climate-dependency models used here are

500   too simple for determining stock status for management (O'Leary *et al.* 2018), but rather serve to

501   demonstrate the relative ramifications of different climate-dependencies when using time-

502   varying reference points. Thus, values should be interpreted only in comparison to the other

503   BRPs in this study, with the knowledge that the climate-natural mortality model was the best

504   performing model for this particular stock.

505   The differences in BRP uncertainty and variability for both approaches and climate-

506   dependencies may be greater if we calculate BRPs for a fish stock with more variable

507   productivity, productivity closer to a threshold tipping point, or with a greater magnitude

508   response to climate. This is particularly relevant for the current management process in many

509   regions, where BRPs include temporal variation by conditioning them on information and stock

510   assessment estimates from the most recent years. Therefore, we suggest that there should be a

511   consultative, iterative process with stakeholders to identify the method used to calculate BRPs.

512   As well, plausible climate hypotheses should be developed and used to test climate-dependencies

513   relevant to the managed fish stock. Researchers can then optimize management procedures based

514   upon the BRP input used for management practices. We suggest incorporating the following

515   steps into management:

516   1. Consider the method of incorporating time-variation into the BRP calculation before

517   harvest control rules and management proceeds. 2. Evaluate how both the dynamic- and

518   moving-average-BRP approaches influence the BRP calculation based on the longevity

519   and time-varying population dynamics of the fish stock. Comparing various BRPs

520   calculated with different modes of temporal variability incorporation is central to

521   understanding the ramifications of any model choice for management.

522   3. Following these two BRP calculations, if a Bayesian assessment model is used, a direct

523   comparison between the BRP posterior distributions can be used to determine the

524   likelihood of overfishing a fish stock. We suggest performance measures to compare

525   between BRP outcomes include average catch, revenue, and avoidance of fishery

526   collapse. A simulation study can be used to determine the trade-off of these performance

527   measures for each BRP decision and identify control rules that balance the competing

528   objectives of the fishery, similar to the Wiedenmann *et al.* (2013) approach used for data-

529   poor fisheries.

530   4. Take into account the timeline and management goals of the various stakeholders to

531   determine how to incorporate BRP uncertainty, variability, and probability of overfishing

532   the stock. A 'stable' reference point does not necessarily imply the 'best' advice. For

533   example, the assessment for summer flounder occurs every 5 years and the Acceptable

534   Biological Catch (ABC) is set every 3 years. In this case, the moving-average-BRPs are

535   more uncertain. Therefore, we advise using these moving-average BRPs over a longer

536   time frame to more cautiously approach 3- 5 year management timeframe of a fish stock

537   whose natural mortality temporally varies from year-to-year. Using this moving-average

538   approach, a fish stock's temporally varying life history and productivity conditions are

539   more likely captured by the greater uncertainty.

540   These steps can be used to extend the time-varying BRP methods established here to

541 provide a quantitative understanding of the risk associated with each BRP decision. Simulation

542 studies to directly compare and evaluate the implications of BRP temporal variability

543 incorporation and climate-dependencies on time-varying BRP calculations for their stock of

544 interest would greatly advance this study.

545   The use of time-varying biological inputs can smooth the effects of population dynamics

546 over adjacent years and across cohorts, making emergent trends challenging to interpret. Despite

547   this limitation, this study provided evidence that temporally-varying climate-inclusive BRP

548   calculations resulted in changes in BRP values over time, but did not cause such a large increase

549   in uncertainty to make BRPs uninterpretable. We also successfully incorporated time-varying

550   parameters using two different methods without making BRPs uninterpretable, providing a

551   method to account for variability and evaluate the risk of multiple scenarios in management as

552   climate conditions continue to change. Importantly, the uncertainty in the time-varying BRPs

553   would likely increase if forecasted, particularly in cases where climate is incorporated into the

554   time-varying population processes (Miller *et al.* 2016). Differences in stock status that depend on

555   the climate-model used highlight the need to account for the effects of changing climate

556   conditions on stock productivity if present.

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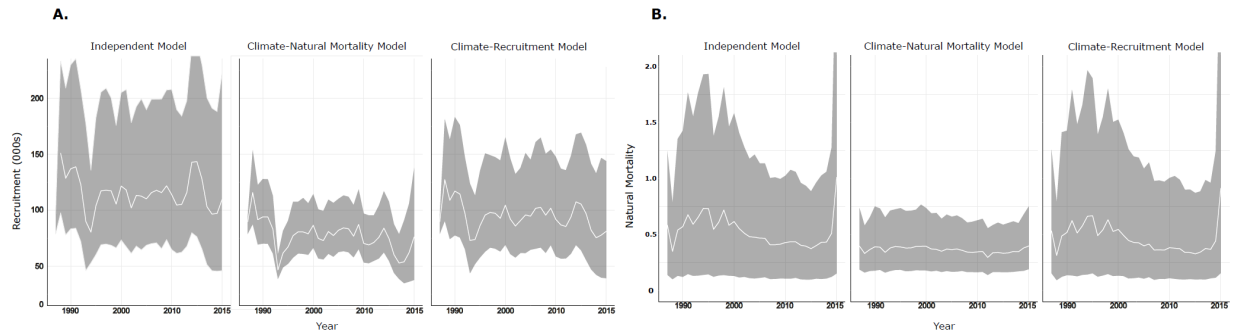571

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591   **Figures**

592
593   **Figure 1.** Weight-at-age from 1982 to 2015 used in all three estimation models. Data was
594   extracted from the summer flounder stock-assessment tables (Terceiro 2016).
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596
597 **Figure 2.** Estimates of recruitment (A) and age 4 natural mortality (B) from 1982 - 2015 for the
598 three climate models, independent (CI), climate-dependent natural mortality (CM), and climate-
599 dependent recruitment (CR), surrounded by 95% credible intervals.
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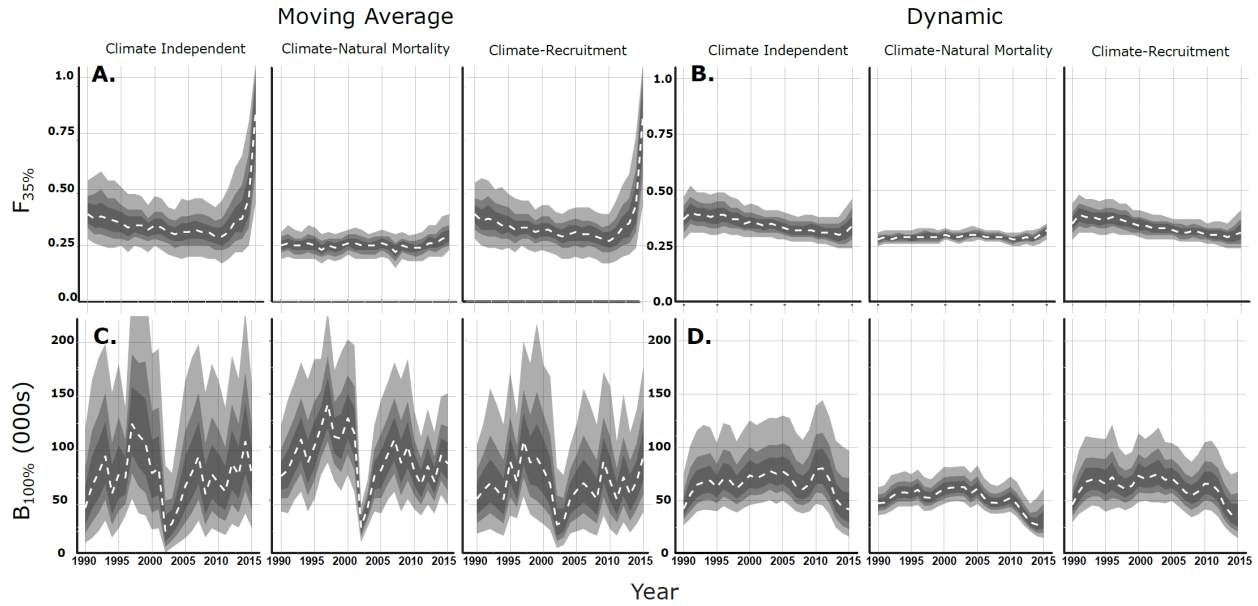
Figure 3. Moving-average-$F_{35\%}(t)$ (panel A), dynamic-$F_{35\%}(t)$ (panel B), moving-average-$B_0(t)$ in mt (panel C), and dynamic-$B_0(t)$ in mt (panel D) for climate-independent (CI), climate-dependent natural mortality (CM), and the climate-dependent recruitment (CR) models for $t = 1990 - 2015$ with $\pm 50\%$ credible intervals, $\pm 75\%$ credible intervals, and $\pm 95\%$ credible intervals from darkest to lightest grey.

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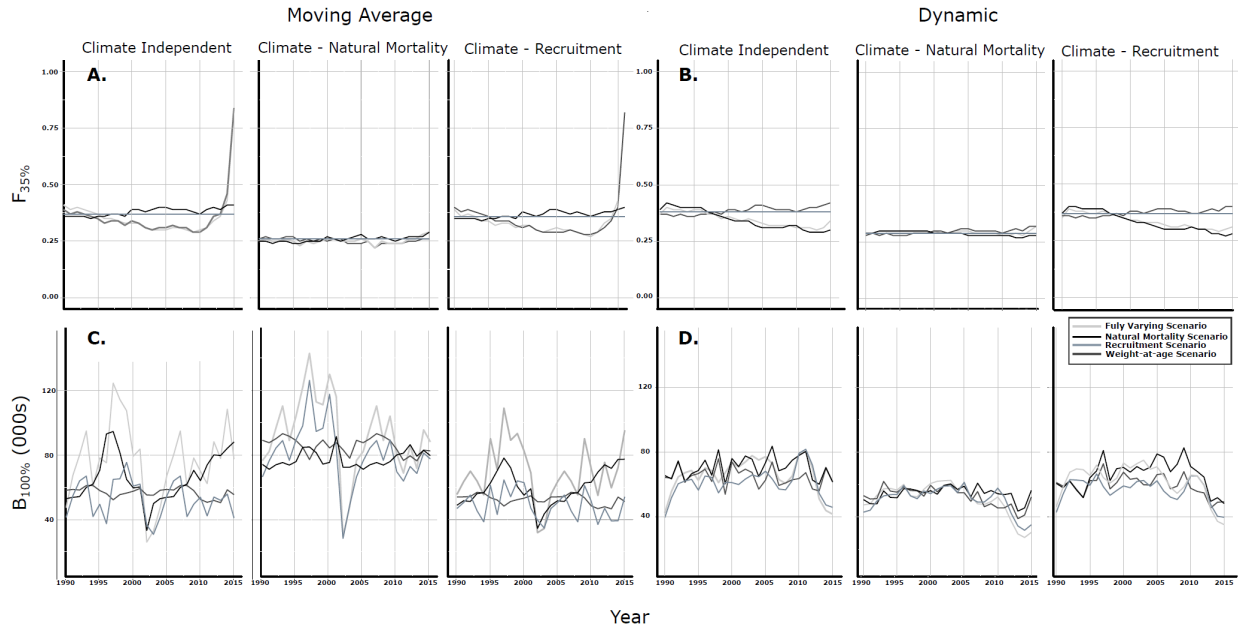
Figure 4. The fully varying BRPs compared to BRPs from three sensitivity analyses attributing
change to varying weight-at-age, varying natural mortality, or varying recruitment in isolation
while holding all other parameters at their average values.
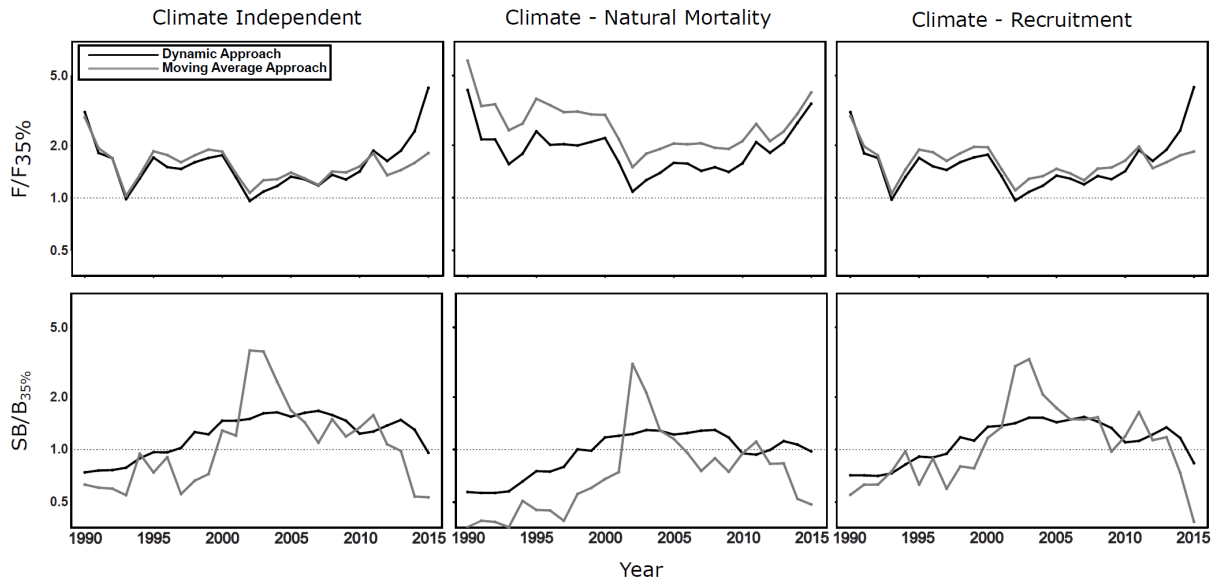
Figure 5. Moving-average-BRP (grey lines) and dynamic-BRP (black lines) stock status plots for the climate independent (CI), climate-natural mortality (CM), and climate-recruitment (CR) models. Plots show (top row) estimated instantaneous fishing mortality (F) divided by $F_{35\%}(t)$ across time and (bottom row) the estimated spawning stock biomass (SB) divided by $B_{35\%}(t)$ across time. A fishing mortality ratio above one indicates overfishing of the stock and below one indicates no overfishing. A spawning stock biomass ratio below one indicates the stock is overfished and above one indicates the stock is not overfished. Note that y-axis is plotted using a log-scale.

622   **Tables**

623

624   **Table 1.** Biological reference point (BRP) definitions and equations. F^* is the instantaneous

625   fishing mortality, t is the year, $\boldsymbol{\theta}_r$ is a sample from the posterior distribution of parameters, $\boldsymbol{n}_r$ is

626   the total number of posterior samples, $\boldsymbol{R}_{t,\mathbf{r}}$ is recruitment in year t for posterior sample r, and

627    $\boldsymbol{SBPR}(F^*|\boldsymbol{\theta}_r, \boldsymbol{t})$ is the spawning biomass per recruit under F^* moving-average on year t and

628   posterior distribution $\boldsymbol{\theta}_r$.

BRP	Definition	Equation	
		Moving-average	**Dynamic**
$F_{35\%}(t)$	The fishing mortality value in year t for posterior sample $\boldsymbol{\theta}_r$ at which spawning biomass per recruit is 35% of the unfished spawning biomass per recruit, given parameters defined in a single year t	For a given F^* in year t $$0.35 = \frac{SBPR(F^*|r,t)}{SBPR(F^*=0|r,t)}$$	For a given F^* in year t, $$0.35 = \frac{SBPR(F^*|\boldsymbol{\theta}_r,t)}{SBPR(F^*=0|\boldsymbol{\theta}_r,t)}$$
$B_0(t)$	The spawning biomass in year t for posterior sample r from past recruitment deviations in the absence of fishing given estimated parameters for stock productivity $\boldsymbol{\theta}_r$	$$\frac{1}{n(r)} \sum_{r=1}^{n(r)} SB(F^*=0|r,t)$$	The spawning biomass when there is no fishing pressure (F^*) in year t, $$SB(F^*=0|r,t)$$

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640   **Table 2.** BRPs using moving-average-BRP and dynamic-BRP approach mean $F_{35\%}(t)$ $F_{35\%}(t)$
641   uncertainty, $F_{35\%}(t)$ temporal variability, mean $B_0(t)$, $B_0(t)$ uncertainty, and $B_0(t)$ temporal
642   variability across years 1990-2015 for the climate recruitment (CR), climate mortality (CM), and
643   climate independent (CI) models. Uncertainty in $F_{35\%}(t)$ and $B_0(t)$ is expressed as the average
644   coefficient of variation and variability in $F_{35\%}(t)$ and $B_0(t)$ is expressed as the coefficient of
645   variation over time.
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		Moving-average			Dynamic		
		CR	**CM**	**CI**	**CR**	**CM**	**CI**
$F_{35\%}(t)$	**mean**	0.35	0.25	0.37	0.34	0.29	0.35
	uncertainty	0.19	0.13	0.20	0.1	0.05	0.11
	variability	0.32	0.14	0.32	0.13	0.06	0.14
$B_0(t)$	**mean (mt)**	70016	83544	76938	63988	52037	68877
	uncertainty	0.46	0.26	0.53	0.25	0.16	0.3
	variability	0.49	0.40	0. 56	0. 28	0.24	0.32

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652 **Table 3.** Variability in $F_{35\%}(t)$ and $B_0(t)$ estimates using moving-average-BRP and dynamic-
653 BRP approach and varying natural mortality (Natural Mortality Scenario), varying weight-at-age
654 (Weight-at-Age Scenario), or varying recruitment (Recruitment Scenario) across years 1990-
655 2015 for the climate recruitment (CR), climate mortality (CM), and climate independent (CI)
656 models. Variability in $F_{35\%}(t)$ and $B_0(t)$ is expressed as the coefficient of variation over time.
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$F_{35\%}(t)$	Moving-average			Dynamic		
	CR	CM	CI	CR	CM	CI
Natural Mortality Scenario Variability	0.35	0.14	0.35	0.15	0.06	0.16
Weight-at-Age Scenario Variability	0.06	0.06	0.07	0.05	0.05	0.05
Recruitment Scenario Variability	0.04	0.03	0.05	0.02	0.02	0.02
$B_0(t)$	Moving-average			Dynamic		
	CR	CM	CI	CR	CM	CI
Natural Mortality Scenario variability	0.45	0.27	0.51	0.15	0.09	0.12
Weight-at-Age Scenario Variability	0.15	0.11	0.16	0.11	0.11	0.09
Recruitment Scenario variability	0.23	0.28	0.28	0.28	0.22	0.35

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663 **References**
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