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Abstract

19 In marine management, fish stocks are often managed on a stock-
20 by-stock basis using single-species models. Many of these models are
21 based upon statistical techniques and are good at assessing the cur-
22 rent state and making short-term predictions; however, as they do
23 not model interactions between stocks, they lack predictive power
24 on longer timescales. Additionally, there are size-based multi-species
25 models that represent key biological processes and consider interac-
26 tions between stocks such as predation and competition for resources.
27 Due to the complexity of these models, they are difficult to fit to data,
28 and so many size-based multi-species models depend upon single-
29 species models where they exist, or *ad hoc* assumptions when they
30 don't, for parameters such as annual fishing mortality.

31 In this paper we demonstrate that by taking a state-space ap-
32 proach, many of the uncertain parameters can be treated dynami-
33 cally, allowing us to fit, with quantifiable uncertainty, size-based multi-
34 species models directly to data. We demonstrate this by fitting un-
35 certain parameters, including annual fishing mortality, of a size-based
36 multi-species model of the Celtic Sea, for species with and without
37 single-species stock-assessments. Consequently, errors in the single-
38 species models no longer propagate through the multi-species model
39 and underlying assumptions are more transparent.

40 Building size-based multi-species models that are internally consis-
41 tent, with quantifiable uncertainty, will improve their credibility and
42 utility for management. This may lead to their uptake by being ei-
43 ther used to corroborate single-species models; directly in the advice
44 process to make predictions into the future; or used to provide a new

45 way of managing data-limited stocks.

46 **Keywords:** Bayesian Statistics; MCMC; Mechanistic models; Multi-
47 species modelling; Uncertainty quantification; State-space approach;
48 Size-based modelling;

49 **1 Introduction**

50 **2 Methods**

51 2.1 State-space model

52 2.2 Data

53 2.3 Fitting the model

54 **3 Results**

55 3.1 Posterior distributions

56 3.2 Spawning stock biomass

57 **4 Discussion**

58 4.1 Integrating size-based multi-species models within man-
59 agement

60 4.2 Further challenges

61 4.3 Quantifying uncertainty

62 4.4 Conclusion

63 **1 Introduction**

64 Food security has been highlighted as one of the major global chal-
65 lenges, with fisheries and aquaculture identified as key contributors to
66 addressing this challenge (FAO, 2009; Frid & Paramor, 2012). Cur-
67 rently the majority of fish stocks are managed using single-species

68 models (SSMs), such as the state-space assessment model (SAM)
69 (Nielsen & Berg, 2014) and projections are made to assess the utility
70 of management decisions. Interacting stocks, which may compete with
71 or predate on one another, can make conventional single-species man-
72 agement difficult (Tyrrell *et al.*, 2011; Quárou & Tomini, 2013; Farcas
73 & Rossberg, 2016). Alternatively a multi-species or whole ecosystem
74 approach could be adopted to account for these interactions (Pikitch
75 *et al.*, 2004; Link *et al.*, 2011; Plagányi *et al.*, 2014). There are sev-
76 eral multi-species models (MSMs) ranging from statistical models (e.g.
77 Stochastic MSM (SMS) Lewy & Vinther, 2004), to more mechanistic-
78 based models (e.g. mizer; Scott *et al.*, 2014) or whole ecosystem models
79 (e.g. StrathE2E; Heath, 2012).

80 SSMs and statistical MSMs are often used to describe the current
81 and recent status of the system, and to make short-term forecasts.
82 They aim to learn about the system by fitting many ‘tuning param-
83 eters’, parameters that are adjusted to make the model look like the
84 observed system (Plagányi *et al.*, 2014; Brynjarsdóttir & O’Hagan,
85 2014). On the other hand, mechanistic models, sometimes called
86 process-based models, are based on the theoretical understanding of
87 the relevant ecological processes (Cuddington *et al.*, 2013). They gen-
88 erally model the behaviour of the system through differential equa-
89 tions and/or a series of rules or algorithms. They prioritise realism
90 over reality, often explaining why things happen rather than describing
91 what happened (White & Marshall, 2019). Many of the parameters
92 are treated as ‘input variables’, with values taken from other sources
93 (Brynjarsdóttir & O’Hagan, 2014), leaving fewer ‘tuning parameters’
94 that represent processes that are either too complex or not known,

95 e.g. recruitment. For example, in size-based MSMs, the predator-prey
96 mass ratio is an ‘input variable’, coming from other studies (e.g. Hat-
97 ton *et al.*, 2015), whereas in statistical MSMs it is treated as a ‘tuning
98 parameter’ and learned from data (e.g. ICES, 2017a) (see Supplemen-
99 tary material S5 for an illustrative example of ‘tuning parameters’ and
100 ‘input variables’).

101 An increasingly popular class of mechanistic models are size-based
102 MSMs (e.g. Blanchard *et al.*, 2014; Szuwalski *et al.*, 2017). Often these
103 models are fitted to, or rely on inputs from, SSMs (e.g. Speirs *et al.*,
104 2016). A common example is instantaneous fishing mortality values
105 that are taken from SSMs, to drive fishing dynamics in MSMs (e.g.
106 Spence *et al.*, 2016). In some ecoregions, fishing mortality values from
107 SSMs either do not exist for all species or only qualitative patterns are
108 reported. In studies with MSMs, fishing dynamics for species without
109 fishing mortality values from SSMs are added using *ad hoc* methods
110 (Jacobsen *et al.*, 2017). Further, as models are simplifications of reality
111 and often the fishing mortality is treated as a ‘tuning parameter’,
112 the fishing mortality values lose their interpretation outside of the
113 fitted model (Rougier & Beven, 2013). Thus they are not the same as
114 the true instantaneous fishing mortality values but instead are model
115 specific. For example statistical MSMs, that are often used to generate
116 natural mortality values for SSMs, have different fishing mortality
117 than the SSMs (e.g. North Sea Cod in SMS and SAM; ICES, 2017a,
118 2018b), despite being fitted to the same data and having a similar
119 representation of the population structure. Fitting MSMs to SSMs
120 or taking inputs from them can lead to circularity in results as errors
121 propagate through the models (Brooks & Deroba, 2015).

122 In MSMs, fitting fishing can be a challenging task. Recent soft-
123 ware advances (e.g. ADMB (Fournier *et al.*, 2012)) have meant that
124 statistical MSMs, designed with tractability in mind, are relatively
125 easy to fit. For size-based MSMs, evaluating the output of a model
126 for a particular set of inputs can often only be done by running the
127 model, which can take anything from a few seconds to a few hours.
128 This means that fitting a large number of uncertain parameters, such
129 as fishing mortality for each year, can be a difficult task. Further-
130 more, for these models to be any use to support management, outputs
131 need to be reported with robust estimates of uncertainty (Harwood &
132 Stokes, 2003).

133 Parameter uncertainty has previously been done in size-based MSMs
134 to explore a handful of parameters (Thorpe *et al.*, 2015). Spence *et al.*
135 (2016) fitted a model of the North Sea using a Bayesian framework,
136 which we adopt here (Bayes, 1763), using Markov chain Monte Carlo
137 (MCMC) to sample from the posterior distribution (Metropolis *et al.*,
138 1953; Hastings, 1970). Adding dynamical parameters, such as annual
139 fishing mortality, makes the uncertain parameter space very large,
140 which makes it difficult to explore. However, we may be able to con-
141 sider the model as a state-space model, a common approach in SSMS
142 (see Aeberhard *et al.*, 2018, for a recent review). In state-space models,
143 the ‘state’ of the system is updated using a Markov process, known as
144 the process model, and there are some noisy, possibly incomplete, ob-
145 servations of the ‘state’, defined by an observation model. For example
146 in many SSMS, such as SAM, the ‘state’ is the numbers of individuals
147 at all ages, at each time-step. In size-based MSMs, we consider the
148 ‘state’ to be the density or numbers of fish and background resource at

149 all sizes at each time-step. State-space models have a specific depen-
150 dence structure (see Figure 1), with the observations of the past and
151 present being conditionally independent given the unobserved state, a
152 structure that can be advantageous when fitting the model (Zucchini
153 *et al.*, 2016).

154 There are many methods of fitting non-linear state-space models
155 including Extended Kalman Filers (Evensen, 2003; Wan & Van Der
156 Merwe, 2000), MCMC methods (Jonsen *et al.*, 2005) and using the
157 Laplace approximation (Tierney & Kadane, 1986) to integrate out
158 the unobserved states (Skaug & Fournier, 2006). Spence *et al.* (2018)
159 used particle filters (Gordon *et al.*, 1993; Liu & Chen, 1998) to update
160 a few years of fishing rates in two MSMs, but for longer periods of
161 time this method is not practical. This is due to the likelihood being
162 largely dominated by the process model and not the observation model
163 which leads to poor mixing of the MCMC (Fasiolo *et al.*, 2016). In
164 this paper we develop an MCMC algorithm that sequentially updates
165 each dynamical parameter and improves the mixing of the MCMC.

166 In many cases the only way of evaluating the likelihood of param-
167 eter values is to run the model. Running size-based MSMs can be
168 slow so ideally one would want to parallelise the model when fitting to
169 data; however this is difficult for MCMC, as iterations need to be done
170 sequentially (Jacob *et al.*, 2011). Some MCMC algorithms have been
171 developed that take advantage of parallel computing (Cui *et al.*, 2011;
172 Calderhead, 2014), whereas others reduce the number of times that
173 the model needs to be run. The delayed-acceptance MCMC algorithm
174 (Sherlock *et al.*, 2017) uses a fast approximation of the likelihood, ei-
175 ther a simplified mechanistic model or a purely statistical one, before

176 deciding whether or not to run the size-based MSM. Due to the high
177 dimensionality of this problem, fitting accurate fast approximations of
178 the likelihood can be difficult, but for many of these problems there
179 are some parameters that affect only part of the likelihood. Here we
180 introduce a second new MCMC algorithm that runs several proposals
181 in parallel using the size-based MSM and then combines them to give
182 a single proposal that has an increased chance of being accepted.

183 In this paper we fit fishing mortality and other uncertain parame-
184 ters of a size-based MSM for the Celtic Sea, without the use of SSMs.
185 We compare stock-assessments made using the model with those de-
186 veloped using SSMs. Although demonstrated on a multi-species ma-
187 rine model, this problem is not unique to MSMs and methods demon-
188 strated here can be used for fitting models of intermediate complexity,
189 e.g. individual-based models (Railsback & Grimm, 2011), especially
190 when there are dynamic parameters. In Section 2 we define state-
191 space models, describe the size-based MSM, the data and the fitting
192 procedure as well as the two new MCMC algorithms. In Section 3
193 we describe the results of the fitted model and we conclude with a
194 discussion in Section 4. We also demonstrate the fitting procedure
195 with a simulation study using another size-based MSM (Spence *et al.*,
196 2020b) in the Simulation study.

197 2 Methods

198 In this section we describe how we can treat the MSM as a state-
199 space model. We introduce the MSM used in this study, the uncertain
200 parameters, which include fishing mortality for each species for each

201 year, and the data to which the model was fitted. We then describe
202 the steps used to sample from the posterior distribution using Markov
203 Chain Monte Carlo (MCMC).

204 **2.1 State-space model**

205 Let M_t , the density of all species, $N_i(m)$, and the background resource,
206 $N_R(m)$ at all weights, m (see Supplementary material S1 for details),
207 be the state of the MSM at time t . Then

$$M_t|M_{t-1} \sim h(M_{t-1}, \phi_t, \theta),$$

208 where ϕ_t are dynamical parameters at time t and θ are static paramete-
209 rs. $h(\cdot)$ is known as the process model. We do not observe the state
210 directly but at time t we observe \mathbf{y}_t , where

$$\mathbf{y}_t|M_t \sim g(M_t, \sigma^2),$$

211 and σ^2 are static parameters. $g(\cdot)$ is known as the observation model.
212 Figure 1 represents this model as a directed acyclic graph (DAG).

213 **Process model**

214 The process model $h(\cdot)$ used here is the deterministic multi-species
215 size-based model, mizer (Hartvig *et al.*, 2011; Scott *et al.*, 2014). Mizer
216 was developed to represent the size and abundance of all organisms
217 from zooplankton to large fish predators in a size-based food web.
218 Some species are represented by species-specific traits and body size
219 while others are represented solely by body size. The core of the model
220 involves ontogenetic feeding and growth, mortality, and reproduction
221 driven by size-dependent predation and maturation processes. The

222 smallest individuals in the model do not eat fish belonging to the fish
223 populations, but consume smaller planktonic or benthic organisms
224 which we describe as a background resource spectrum. Fish grow and
225 die according to size-dependent predation and, if mature, recruit new
226 young which are put back into the system at the minimum weight. As
227 well as the predation and background mortality, the fish in the model
228 also experience fishing mortality.

229 In this study we fit mizer for 17 species, shown in Table 1, in
230 the Celtic Sea, ICES (International Council for Exploration of the
231 Seas) areas 7e-j. A description of the model can be found in the
232 Supplementary material (S1) along with the parameter values.

233 In mizer there are a number of uncertain parameters to estimate.
234 The carrying capacity of the background resource spectrum, κ , is un-
235 certain, with a relatively uninformative prior distribution given by
236 $\ln(\kappa) \in [0, 40]$ uniformly (see Table 2). Recruitment follows a density-
237 dependent process with the maximum number of recruits of the i th
238 species being $R_{max,i}$, which is also uncertain. We specified a relatively
239 uninformative prior distribution as $\ln(R_{max,i}) \in [0, 50]$ uniformly (see
240 Table 2), for all i . The fishing mortality of the i th species of weight
241 m at time t was

$$\phi_{t,i}q_i(m),$$

242 where $q_i(m)$ is the catchability of species i at size m , normalised so
243 that $\max_m(q_i(m)) = 1$, and $\phi_{t,i}$ is the fishing rate (values for $q_i(m)$
244 are shown in the Supplementary material (Figure S1)). The model
245 was run from 1991-2014 ($t = 1, \dots, 24$) and the fishing rate for each
246 species for each year was also uncertain with $\phi_{t,i} \in [0, 1.5]$ uniformly
247 for $t = 1, \dots, 24$ and for all i .

248 The model can be sensitive to its initial state, when $t = 0$, and so
 249 the model was projected for 300 years to a stationary state, a process
 250 known as spin-up, with a fixed fishing rate $\phi_{0,i}$ for each species prior
 251 to running for $t = 1, \dots, 24$. As in Spence *et al.* (2016) we treated the
 252 spin-up fishing rates as additional parameters with $\phi_{0,i} \in [0, 1.5]$ uni-
 253 formly for all i (see Table 2). We consider $\boldsymbol{\theta} = (\ln \kappa, \ln R_{max,1:17}, \phi_{0,1:17})'$
 254 to be ‘static’ parameters and the fishing rates, $\phi_{1:24,1:17}$ to be ‘dynam-
 255 ical’ parameters (with 1:17 meaning $i = 1 \dots 17$).

256 In addition to the commercial fishing mortality, we included survey
 257 fishing mortality. The catchability of the survey vessel was taken
 258 from Walker *et al.* (2017) and the fishing effort for the survey effort
 259 taken from DATRAS (ICES, 2017b). By including the survey fishing
 260 mortality we are able to fit the model to data from survey.

261 Observation model

262 At time t , we observe catches in tonnes, \mathbf{y} , made up of those by
 263 commercial vessels, \mathbf{w}_t for $t = 1, \dots, 24$ (1991-2014), and those by
 264 the International Bottom Trawl Survey (IBTS), \mathbf{z}_t for $t = 7, \dots, 24$
 265 (1997-2014), with $|\mathbf{w}_t| = |\mathbf{z}_t| = 17$. We take

$$\ln \mathbf{w}_t \sim N(\ln \mathbf{c}(M_t), \Sigma_c)$$

266 where $\mathbf{c}(M_t)$ is the commercial catch from the process model and Σ_c
 267 is a diagonal matrix with elements σ_c^2 . Similarly we take

$$\ln \mathbf{z}_t \sim N(\ln \mathbf{s}(M_t), \Sigma_s)$$

268 where $\mathbf{s}(M_t)$ is the survey catch from the process model and Σ_s is
 269 a diagonal matrix with elements σ_s^2 . The i th elements of $\mathbf{c}(M_t)$ and
 270 $\mathbf{s}(M_t)$ are denoted $c(M_t)_i$ and $s(M_t)_i$ and defined in equations S3 and

271 S4 in the Supplementary material respectively. The likelihood of the
 272 model is

$$\begin{aligned}
 l(\mathbf{y}|\boldsymbol{\theta}, \phi_{1:24,1:17}, \boldsymbol{\sigma}_c^2, \boldsymbol{\sigma}_s^2) &= \prod_{i=1}^{17} \prod_{t=1}^{24} N(\ln(w_{t,i}) | \ln(c(M_t)_i), \sigma_{c,i}^2) \\
 &\quad \times \prod_{t=7}^{24} N(\ln(z_{t,i}) | \ln(s(M_t)_i), \sigma_{s,i}^2), (1)
 \end{aligned}$$

273 where $w_{t,i}$, $z_{t,i}$, $\sigma_{c,i}^2$ and $\sigma_{s,i}^2$ are the i th element of \mathbf{w}_t , \mathbf{z}_t , $\boldsymbol{\sigma}_c^2$ and
 274 $\boldsymbol{\sigma}_s^2$ respectively, and $N(a|d, e)$ is a normal density with expectation
 275 d and variance e evaluated at a . Table 2 summarises the uncertain
 276 parameters.

277 2.2 Data

278 Landings data were extracted from ICES (ICES, 2017c) and discards
 279 were estimated as a percentage of the retained biomass (Heymans
 280 *et al.*, 2016; Anon, 2015). All discards were assumed to have been
 281 removed from the living stock in the process model, such that all
 282 discards are assumed to have died. As only discards and no landings
 283 were recorded for poor cod and Norway pout, we fixed the variance of
 284 the commercial catches, $\sigma_{c,7:8}^2 = (4, 4)'$ (Farnsworth *et al.*, 2014). We
 285 extracted the IBTS survey data from DATRAS (ICES, 2017b) from
 286 1997 until 2014 ($t=7, \dots, 24$).

287 2.3 Fitting the model

288 The model was fitted in a Bayesian framework so that we could quan-
 289 tify the uncertainty in the model parameters using probability. As
 290 the likelihood was intractable we were required to sample from the
 291 posterior distribution. Although a suitable Markov Chain with sta-

292 tionary distribution equal to the posterior would eventually converge
293 to the posterior distribution, this would take a long time. To speed
294 the process up we aimed to start the Markov chain close to the high-
295 probability region of the posterior distribution. To find these starting
296 values we used history matching to reduce the parameter space (Ver-
297 non *et al.*, 2014).

298 **Markov Chain Monte Carlo**

299 The posterior distribution was explored using MCMC. Due to the high
300 dimensionality of the parameter space, mixing efficiently was difficult
301 and so we developed two extensions of the delayed-acceptance MCMC
302 algorithm of Sherlock *et al.* (2017) that take advantage of parallel
303 computing and explore the posterior distribution in an efficient way.

304 The first extension, which we refer to as the marginal-delayed-
305 acceptance MCMC (MDA-MCMC), is shown in Algorithm 1. It is
306 understood that when moving in smaller dimensions it is possible to
307 make larger moves (Neal & Roberts, 2006); here we propose several
308 moves in smaller dimensions and check their suitability before trying
309 to make the full dimensional move. For each iteration the parameter
310 set is divided into $N + 1$ disjoint sets with N of the sets each hav-
311 ing some likelihood function, $l_i(\cdot)$, associated with it. This algorithm
312 attempts to update the parameters in the first N sets whilst holding
313 the parameters in the $N + 1$ set, which may be empty, fixed. N of the
314 parameter sets are each updated by one iteration of the Metropolis-
315 Hastings MCMC algorithm, keeping the other parameters fixed, with
316 its own likelihood function. If the current model run is saved, this
317 would cost N new model evaluations ($N + 1$ if not) that could be done

Algorithm 1 An iteration of the marginal-delayed-acceptance MCMC algorithm (MDA-MCMC). The current parameters $\boldsymbol{\theta}$, are divided into $N + 1$ disjoint sets with the i th set being denoted $\boldsymbol{\theta}_i$, having the likelihood evaluation $l_i(\mathbf{y}|\boldsymbol{\theta})$ and proposal distribution $f_i(\cdot|\boldsymbol{\theta}_i)$. $p(\boldsymbol{\theta})$ is the prior and $l(\mathbf{y}|\boldsymbol{\theta})$ is the full likelihood. We define \wedge to be the minimum, i.e. $a \wedge b = \min(a, b)$.

$\boldsymbol{\theta}'' \leftarrow \boldsymbol{\theta}$

for i in $1 : N$ **do**

$\boldsymbol{\theta}'_i \sim f_i(\cdot|\boldsymbol{\theta}_i)$

$\boldsymbol{\theta}''_i \leftarrow \boldsymbol{\theta}'_i$ with probability

$$\alpha_i(\boldsymbol{\theta}, \boldsymbol{\theta}'_i) = 1 \wedge \frac{p(\boldsymbol{\theta}'_i)l_i(\mathbf{y}|\boldsymbol{\theta}'_i, \boldsymbol{\theta}_{-i})}{p(\boldsymbol{\theta}_i)l_i(\mathbf{y}|\boldsymbol{\theta})}$$

end for

$\boldsymbol{\theta} \leftarrow \boldsymbol{\theta}''$ with probability

$$\begin{aligned} & 1 \wedge \frac{p(\boldsymbol{\theta}'')l(\mathbf{y}|\boldsymbol{\theta}'')}{p(\boldsymbol{\theta})l(\mathbf{y}|\boldsymbol{\theta})} \\ & \times \prod_{\{i:\boldsymbol{\theta}''_i \neq \boldsymbol{\theta}_i\}} \frac{f_i(\boldsymbol{\theta}_i|\boldsymbol{\theta}'_i)}{f_i(\boldsymbol{\theta}'_i|\boldsymbol{\theta}_i)} \times \frac{\alpha_i(\boldsymbol{\theta}'', \boldsymbol{\theta}_i)}{\alpha_i(\boldsymbol{\theta}, \boldsymbol{\theta}_i)} \\ & \times \prod_{\{i:\boldsymbol{\theta}''_i = \boldsymbol{\theta}_i\}} \frac{1 - \alpha_i(\boldsymbol{\theta}'', \boldsymbol{\theta}_i)}{1 - \alpha_i(\boldsymbol{\theta}, \boldsymbol{\theta}_i)} \end{aligned}$$

318 in parallel and so could, in terms of clock time, take one model eval-
319 uation. The output from each of the N MCMC algorithms is used as
320 a proposal for the main MCMC algorithm. This then takes a further
321 two new model evaluations which could be performed in parallel. Us-
322 ing the acceptance rates described in Algorithm 1 leads to a Markov
323 Chain with the correct stationary distribution, a proof of which is in
324 the Supplementary material (S3).

325 The second extension, which we call particle-delayed-acceptance
326 MCMC (PDA-MCMC), is shown in Algorithm 2. In PDA-MCMC
327 the fishing rates for each year are sequentially updated using the
328 Metropolis-Hastings algorithm. Once the algorithm has updated for
329 each year of the model, the new fishing rates are used as a proposal
330 for the MCMC update. This requires five model runs, which could
331 be as quick as two model runs in terms of clock time (as the four of
332 the model runs could be parallelised) and leads to a Markov Chain
333 with the correct stationary distribution, a proof of which is in the
334 Supplementary material (S3).

335 To sample from the whole posterior distribution we used a ran-
336 dom walk Metropolis-within-Gibbs algorithm with proposal variances
337 tuned from a pilot run. At each iteration we performed four types of
338 updates:

- 339 1. Update $\ln R_{max,1:17}$ and $\phi_{0,1:17}$ together using the MDA-MCMC
340 algorithm with $N = 17$. The i th set was $\{\ln R_{max,i}, \phi_{0,i}\}$ with

$$l_i(\mathbf{y}|\boldsymbol{\theta}) = \prod_{t=1}^{24} N(\ln(w_{t,i}) | \ln(c(M_t)_i), \sigma_{c,i}^2) \times \prod_{t=7}^{24} N(\ln(z_{t,i}) | \ln(s(M_t)_i), \sigma_{s,i}^2)$$

341 and the full likelihood, $l(\mathbf{y}|\boldsymbol{\theta})$ being $l(\mathbf{y}|\boldsymbol{\theta}, \phi_{1:24,1:17}, \boldsymbol{\sigma}_c^2, \boldsymbol{\sigma}_s^2)$ from
342 equation 1. The 18th set, which does not get updated at this

Algorithm 2 An iteration of the particle-delayed-acceptance MCMC algorithm (PDA-MCMC). Let $M_t = h(M_{t-1}, \phi_{1:17,t}, \boldsymbol{\theta})$ be the model run up until time t , with M_0 being its initial state and $k_t(M_t)$ be a likelihood evaluation of this model. The static parameters are $\boldsymbol{\theta}$, the current fishing rates are $\phi_{1:17,1:24}$ and $f(\cdot|\phi_{1:17,t})$ is the proposal distribution. The full likelihood is $l(\mathbf{y}|\phi_{1:17,1:24})$ and $p(\phi_{1:17,1:24})$ is the prior. We define \wedge to be the minimum, i.e. $a \wedge b = \min(a, b)$.

$Q_0 \leftarrow M_0, \phi''_{1:17,1:24} \leftarrow \phi_{1:17,1:24}$

for t in $1 : 24$ **do**

$\phi'_{1:17,t} \sim f(\cdot|\phi_{1:17,t})$

$M'_t \leftarrow h(M_{t-1}, \phi'_{1:17,t}, \boldsymbol{\theta})$ and $M_t \leftarrow h(M_{t-1}, \phi_{1:17,t}, \boldsymbol{\theta})$

$Q'_t \leftarrow h(Q_{t-1}, \phi'_{1:17,t}, \boldsymbol{\theta})$ and $Q_t \leftarrow h(Q_{t-1}, \phi_{1:17,t}, \boldsymbol{\theta})$

$\phi''_{1:17,t} \leftarrow \phi'_{1:17,t}$ and $M_t \leftarrow M'_t$ with probability

$$\alpha_t(\phi_{1:17,t}, \phi'_{1:17,t}) = 1 \wedge \frac{p(\phi'_{1:17,t})k_t(M'_t)}{p(\phi_{1:17,t})k_t(M_t)}$$

end for

$\phi_{1:17,1:24} \leftarrow \phi''_{1:17,1:24}$ with probability

$$1 \wedge \frac{p(\phi''_{1:17,1:24})l(\mathbf{y}|\phi''_{1:17,1:24})}{p(\phi_{1:17,1:24})l(\mathbf{y}|\phi_{1:17,1:24})} \times \prod_{\{t:\phi_{1:17,t} \neq \phi''_{1:17,t}\}} \frac{f(\phi_{1:17,t}|\phi'_{1:17,t})}{f(\phi'_{1:17,t}|\phi_{1:17,t})} \times \frac{1 \wedge \frac{p(\phi_{1:17,t})k_t(Q_t)}{p(\phi'_{1:17,t})k_t(Q'_t)}}{\alpha(\phi_{1:17,t}, \phi'_{1:17,t})} \times \prod_{\{t:\phi_{1:17,t} = \phi''_{1:17,t}\}} \frac{1 - 1 \wedge \frac{p(\phi'_{1:17,t})k_t(Q'_t)}{p(\phi_{1:17,t})k_t(Q_t)}}{1 - \alpha(\phi_{1:17,t}, \phi'_{1:17,t})}$$

343 step, was $\{\ln(\kappa), \phi_{1:17,1:24}, \sigma_c^2, \sigma_s^2\}$.

344 2. Update $\phi_{1:24,1:17}$ using the PDA-MCMC algorithm. We used
345 eight proposals in parallel using parallel MCMC as in Cui *et al.*
346 (2011). We set

$$k_t(M_t) = \prod_{i=1}^{17} N(\ln(w_{t,i})|c(M_t)_i, \sigma_{c,i}^2)$$

347 for $t = 1, \dots, 6$ and

$$k_t(M_t) = \prod_{i=1}^{17} N(\ln(w_{t,i})|c(M_t)_i, \sigma_{c,i}^2) N(\ln(z_{t,i})|s(M_t)_i, \sigma_{s,i}^2)$$

348 for $t = 7, \dots, 24$.

349 3. We updated $\ln \kappa$ and $\ln R_{max,1:17}$ by proposing several alter-
350 natives and moving between them using Calderhead's parallel
351 MCMC algorithm (Calderhead, 2014).
352 4. We updated σ_c^2 and σ_s^2 using Gibbs samplers.

353 For a description of Cui *et al.*'s and Calderhead's parallel MCMC see
354 the Supplementary material (S2).

355 3 Results

356 The MCMC algorithm was run for 20,000 iterations, dropping the ini-
357 tial 10,000 as burn-in. The convergence of the MCMC was checked
358 visually by examining the traceplots of the parameters (see Supple-
359 mentary material (S4) for traceplots and results of the history match-
360 ing).

3.1 Posterior distributions

Figure 2 shows the variance parameters for the catches and the survey. The variance parameters describe the estimated distribution of the error around the observed catches as well as the model’s inability to predict them. The variance parameters for the catches were much lower than for the survey, particularly for pelagic species, suggesting that the model does a much better job of fitting to commercial catches than the survey data. The model does a good job of capturing the catches of most fish with the exceptions of horse mackerel and blue whiting. This can also be seen in Figure 3 where we show the median, 10th percentile and 90th percentile of the modelled commercial catches compared to the observed landings (see Supplementary material (Figure S16) for a the same plot for the survey catches).

Figure 4 shows the posterior $\phi_{1:17,1:24}$ values for each of the species except Norway pout and poor cod. It also shows the fishing mortality values from the ICES stock-assessments, which use SSM, for cod, haddock, whiting, hake, megrim and herring. The cod, haddock and whiting assessments are for the Celtic Sea (ICES, 2018a,c,g), whereas the hake, megrim and herring assessments are for a larger region than our study (ICES, 2018d,e,f). With the exception of haddock, the $\phi_{1:17,1:24}$ values from this study seem to follow, at least qualitatively, that of the assessment fishing mortality.

Figure 5 shows the marginal posterior distribution of the fishing rate during the spin-up period, $\phi_{i,0}$. Many of the posterior distributions are similar to their prior distributions, e.g. herring, sprat, however some of the posteriors are quite different from their priors. The fishing rates for cod and horse mackerel are low, which means

388 that when the simulation starts in 1991, cod and horse mackerel will
389 be in a nearly unfished state whereas hake and monkfish, which have
390 quite high fishing rates in the spin-up period, start the simulation in
391 an exploited state.

392 **3.2 Spawning stock biomass**

393 Figure 6 shows the median, 10th percentile and 90th percentile esti-
394 mates for cod, haddock, whiting, hake, herring and megrim spawning
395 stock biomass (SSB). It also shows the SSB estimates from ICES stock-
396 assessments using SSMs. The cod assessment and the mizer model
397 agree towards the end of the time period. The whiting single-species
398 and multi-species estimates are similar. Both hake assessments show
399 an increase in SSB at about 2005 which coincides with a reduction
400 in the fishing rate at around the same time, as shown in Figure 4;
401 this is also visible in the stock-assessment. In addition the qualitative
402 patterns in herring and megrim seem similar in both the MSM and
403 the SSM. The MSM predicts different SSB for haddock than the SSM.

404 **4 Discussion**

405 In this study we fitted the size-based MSM of Blanchard *et al.* (2014)
406 with 17 species in the Celtic Sea using novel techniques to address
407 the high dimensionality of the problem. We also demonstrated these
408 methods in a simulation study with three species using the model of
409 Spence *et al.* (2020b), also a size-based MSM (see Simulation study in
410 the supplementary material).

411 We found that the model was able to recreate demersal survey

412 catches and commercial catches. The model was not able to recreate
413 the survey data for pelagic fish. This is understandable as the IBTS
414 survey is not so good at sampling pelagic and flatfish and therefore
415 the noise is much greater (Walker *et al.*, 2017). Our approach gives an
416 idea about the magnitude of the observation uncertainty in the IBTS
417 survey. We could further reduce uncertainty in the model by fitting
418 to additional surveys, for example acoustic surveys.

419 For most of the stocks with full assessments, we get similar SSB and
420 fishing rates, however for haddock both are qualitatively and quan-
421 titatively different. In the SSMs, the recruitment rates of haddock
422 are unpredictable (ICES, 2018c), something that is not captured by
423 the MSM here, which suggests that the SSB in SSMs is recruitment
424 driven. Stochastic recruitment has been included in some size-based
425 MSMs (e.g. Blanchard *et al.*, 2014; Thorpe *et al.*, 2017), but more
426 work is required to explore this.

427 **4.1 Integrating size-based multi-species mod-** 428 **els within management**

429 Before this study, fitting size-based MSMs to species that did not
430 have full assessments with absolute values of the fishing mortality
431 was not possible without making strong assumptions about their fish-
432 ing mortality values (Jacobsen *et al.*, 2017). This would be particu-
433 larly the case for species with limited data (Quárou & Tomini, 2013).
434 The methods of fitting dynamical parameters introduced and demon-
435 strated here could lead to an increase in the number of size-based
436 MSMs for regions where there is not a great amount of information,
437 hence increasing their utility and enhancing the strategic management

438 of these areas. This could either be by sharing fishing rates between
439 other size-based MSMs, for example a LeMans model for the Celtic
440 Sea could use fishing rates from this study, or directly fitting the dy-
441 namical parameters.

442 Although there is such a thing as a true fishing mortality, using it
443 as a ‘tuning parameter’, as done in this study and in many SSMs, de-
444 stroys its true meaning (Rougier & Beven, 2013). For example, in the
445 model we fitted in this study, only the fishing rates were used to drive
446 the dynamics. Therefore, the fishing rates implicitly have information
447 about all things that drive the dynamics of the species, e.g. environ-
448 ment, recruitment or migration. Although many SSMs account for
449 dynamic recruitment (e.g. Stock Synthesis, Methot & Wetzel, 2013),
450 their fishing mortality also imply dynamics caused by interactions be-
451 tween different species, which is explicit in MSMs. Therefore taking
452 fishing mortality values from other models and using them as ‘input
453 variables’ (e.g. Thorpe *et al.*, 2015; Spence *et al.*, 2016; Speirs *et al.*,
454 2016), can lead to systematic biases in the model (Brooks & Deroba,
455 2015) and so should be done with caution, however there are circum-
456 stances when it might actually be desirable. For instance we may wish
457 to save on computational effort, or we may want the fishing rates to
458 represent the fishing mortality generated by stock assessments rather
459 than the actual fishing mortality on the stock, as it is possible to
460 calculate this and manage to it (e.g. Spence *et al.*, 2020a).

461 A common requirement of fisheries models is to assess the current
462 state of a stock. SSMs and statistical MSMs, with many ‘tuning pa-
463 rameters’, are good at doing this when there is a lot of data. However,
464 by fitting size-based MSMs directly to data, we free the model from

465 biases caused by SSMS and could therefore contribute to the assess-
466 ment processes. The natural mortality rates from size-based MSMS
467 could be used as ‘input variables’ to SSMS in regions where there is
468 a lack of data (e.g. stomach contents data), making statistical MSMS
469 impractical. For example, results from this Celtic Sea model could be
470 used to generate natural mortality rates that could be used as inputs
471 to SSMS, as currently natural mortality inputs for many of the Celtic
472 Sea assessments come from a theoretical study (Lorenzen, 1996). For
473 regions where statistical MSMS already exist, size-based MSMS could
474 be used to corroborate or validate them, increasing our confidence in
475 their results, to suggest an alternative or as part of an ensemble model
476 (Collie *et al.*, 2016).

477 More generally, mechanistic models have been increasingly used as
478 strategic tools when considering how populations, communities and
479 ecosystems respond to management or environmental changes (Pik-
480 itch *et al.*, 2004; Collie *et al.*, 2016). They are developed with eco-
481 logical and biological theory, through ‘input variables’ and processes
482 within the model. Therefore, as this theory develops, the mechanistic
483 models become more like reality. As mechanisms and physical laws
484 are time invariant and more robust than statistical correlations, mech-
485 anistic MSMS should enable us to make better long-term predictions
486 as interactions between different species and different processes will
487 be more explicit (Connor *et al.*, 2017; Cuddington *et al.*, 2013). This
488 should lead to improved strategic management, for example in setting
489 long-term targets and reference points, such as multi-species maximum
490 sustainable yield. Improvements in our understanding of responses to
491 new conditions, such as warming oceans, can readily be included in

492 these models (e.g. Serpetti *et al.*, 2017) and the types of actions that
493 can be tested and implemented can be increased, e.g. spatial planning
494 using spatially explicit mechanistic models (e.g. Ecospace, Walters
495 *et al.*, 1999).

496 In addition, mechanistic models could be used to manage data-
497 limited stocks, possibly using life history parameters from other stud-
498 ies (e.g. Thorson *et al.*, 2017), or in areas of the world where there
499 are many species and building MSMs is computationally expensive
500 or managing at the level of individual species is impracticable. This
501 is particularly true for size-based models due to the connection be-
502 tween size-based theory and traits (Andersen, 2020). The methods
503 developed here to find dynamical parameters could be useful when
504 fitting trait-based models, where groups of species with similar traits
505 are grouped together (Barnett *et al.*, 2019).

506 **4.2 Further challenges**

507 Whilst size-based MSMs are potentially powerful tools, their use to
508 date in the advisory process has been limited. Here we suggest some
509 improvements that should make them more useful to fisheries man-
510 agement.

511 In this work the state of the system at the beginning of the simu-
512 lation, M_0 , was determined by running the model for 300 years with
513 a fixed fishing mortality $\phi_{0,1:17}$, known as the spin-up period (Spence
514 *et al.*, 2016). This led to the model starting in a stationary state,
515 something which may not be true and can have an effect on the re-
516 sults of the model, particularly at the beginning of the simulation.
517 For example, cod was probably not in a stationary state in 1991, as

518 prior to the model large landings were reported in 1988-1990 (ICES,
519 2018a). It is not possible to create the effect of these high landings
520 using the spin-up period, and our fitted model is therefore unable to
521 pick up the dynamics at the beginning of the time series. The fitted
522 model found that the spin-up fishing mortality for cod, $\phi_{0,3}$, was low
523 (Figure 5), which lead to over-estimating the SSB (Figure 6) and the
524 fishing mortality (Figure 4) in the early part of the simulation.

525 More work is required calibrating the initial state of size-based
526 MSMs. One may run some dynamics, say ten years, before calibra-
527 tion, however it would not have been possible here as we do not know
528 the fishing mortality rates for 1981-1991; alternatively one could run
529 the fishing mortality time series backwards before starting to fit the
530 data, as done in climate modelling (Stouffer *et al.*, 2004). A com-
531 mon approach in other fisheries models is to treat the initial states
532 as uncertain, i.e. treating the density for each species and the back-
533 ground for all sizes in mizer as uncertain parameters. We believe this
534 would be the ideal solution, however it would lead to an impractically
535 large number of parameters. A more practical solution may be to
536 use ecological theory from other studies, such as fishing effects on the
537 size-spectrum (e.g. Zhang *et al.*, 2018), to parameterise, with only a
538 handful of parameters, the initial state of the model. These parame-
539 ters would then be calibrated to the data as well.

540 In this work we used the default fishing selectivity in mizer (Scott
541 *et al.*, 2014). Other fishing selectivity functions, such as logistic or
542 dome shaped, may lead to different results, however we do not believe
543 that the results would greatly change here. In the future we would
544 like to include fisheries information, such as effort and catch by fleet

545 or metier, and possibly by size, when fitting these models. In addition
546 information from external studies about the selectivity of different
547 fishing gears could be included, with the selectivity of each gear on
548 each species being the ‘tuning parameters’ (e.g. Walker *et al.*, 2017).
549 One may anticipate that the selectivity by size may follow an unknown
550 smooth function, as for two individuals of the same species we would
551 expect a similar selectivity for the same gear if their sizes were similar,
552 as opposed to if they were further apart, thus incorporating more
553 information in the model.

554 With size-based MSMs it is not straightforward to perform con-
555 ventional model validation. In the study here it was not possible to
556 compare the model forecasts with independent out-of-sample data,
557 e.g. the survey and commercial catches in 2015-2019, as the fishing
558 rates, the inputs that are used to drive the dynamics that led to these
559 data, are uncertain. Furthermore, due to the time taken to fit these
560 models it is not practical to perform one-step-ahead analysis (Berg
561 & Nielsen, 2016) or cross-validation tests. Instead we demonstrated
562 through residual analysis that the conditionally independent assump-
563 tions are not violated (see Supplementary material (S4)). There are
564 many other methods that could be used for model validation (e.g. pos-
565 terior predictive checks, see Gelman *et al.*, 2013, for more details); for
566 a recent review of these methods see Conn *et al.* (2018).

567 **4.3 Quantifying uncertainty**

568 For models to be useful for management it is important that uncer-
569 tainty is quantified (Harwood & Stokes, 2003). By fitting the model
570 in a Bayesian framework we were able to quantify the uncertainty in

571 the model. This is a difficult problem using conventional MCMC due
572 to the complexity of the model, and the increased dimension of the
573 uncertain parameters caused by fitting fishing mortality. We believe
574 that this is a major reason why this has not previously been done.
575 SSMs and statistical MSMs take advantage of recent software devel-
576 opments and are fitted using algorithms that exploit gradients, such as
577 Hamiltonian Monte Carlo (Neal, 2010) or Reimann Manifold MCMC
578 (Girolami & Calderhead, 2011). However, for size-based MSMs, this
579 may be impractical or even impossible. In this paper we have demon-
580 strated a method of exploiting the structure of the model to use an
581 MCMC algorithm to fit the size-based MSM.

582 For size-based MSMs, where the model needs to be run to evaluate
583 the likelihood, it is advantageous to use parallel computing, running
584 several likelihood evaluations at once, to speed up the fitting process.
585 The problem here is that MCMC is a sequential algorithm and there-
586 fore difficult to run in parallel (Jacob *et al.*, 2011). In this paper
587 we introduce two novel variations of the delayed-acceptance MCMC
588 algorithm (Sherlock *et al.*, 2017). The MDA-MCMC algorithm is de-
589 signed to use parallel computing and is motivated by attempting to
590 move many parameters at once, accepting the good moves whilst re-
591 jecting the bad ones. We believe that the MDA-MCMC would be most
592 useful when sets of parameters, or transformations of the parameters,
593 affect different parts of the likelihood. This could be explored us-
594 ing variance-based sensitivity analysis (Saltelli *et al.*, 2008) prior to
595 running the algorithm. As the MDA-MCMC algorithm makes moves
596 in smaller dimensions, the proposals can be larger in the parameter
597 space. We recommend the proposals are large so that the resulting

598 acceptance probabilities, in the first part of the algorithm, are either
599 0 or 1. This would mean that the accepted points result in large
600 improvements in the full likelihood.

601 Similarly the PDA-MCMC is motivated by proposing moves in a
602 large number of dynamical parameters but efficiently accepting only
603 the good moves. If one was going to fit the dynamical parameters by
604 hand, one might wish to change the fishing rates one year at a time
605 and to run that model for one year. The PDA-MCMC algorithm does
606 just that but in such a way that the stationary distribution of the
607 Markov chain is the posterior distribution. An alternative would be
608 to change one year at each iteration of the MCMC chain, therefore
609 requiring 24 model runs all of which are required to be done sequen-
610 tially, whereas using the PDA-MCMC algorithm it only requires five
611 model runs, most of which can be run in parallel. This therefore leads
612 to more efficient use of computational effort when updating dynamical
613 parameters such as annual fishing rates. The PDA-MCMC algorithm
614 can also be flexible when deciding which of the dynamical parameters
615 are changed. In the study in the manuscript we attempted to change
616 all of the dynamical parameters at once, however in the Simulation
617 study we only changed a handful of dynamical parameters at a time,
618 something that we found led to better mixing. The PDA-MCMC al-
619 gorithm is also useful when the state of the model is dependent on
620 the entire past and/or is stochastic. To do this one would require
621 M_t to include the whole of the past. If the model was stochastic, we
622 recommend treating the stochastic elements as additional parameters,
623 as in Spence & Blackwell (2016), allowing better exploration of the
624 dynamical parameter space. These two algorithms are not specific to

625 size-based MSMs, or mechanistic models, but are applicable to a wide
626 range of MCMC problems.

627 **4.4 Conclusion**

628 We have demonstrated a method of fitting size-based MSMs directly to
629 data without using SSMs. By using novel techniques we were able to fit
630 a model of intermediate complexity in a high-dimensional parameter
631 space with quantifiable uncertainty. Furthermore, by fitting size-based
632 MSMs directly to data, we free the model from the biases caused by
633 SSMs, which may lead to a greater reliability and trust in size-based
634 MSMs, increasing their utility in the management process.

635 Although demonstrated on two size-based multi-species marine
636 models, this methodology is readily generalisable for fitting models of
637 intermediate complexity (with a typical run time of 1 second to a few
638 minutes), when there are a significant number of uncertain dynamic
639 parameters. It is therefore likely to find wide applications throughout
640 science.

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653 **Authors' contribution**

654 MAS conceived the ideas and designed the methodology; MAS, RTB,
655 and PGB fit the model to the data; RS, FS and JLB developed the
656 model used in the case study; MAS led the writing of the manuscript.
657 All authors contributed critically to the drafts and gave final approval
658 for publication

659 **Data availability statement**

660 Data sharing is not applicable to this article as no new data were
661 created; rather, data were acquired from existing published sources (all
662 sources are cited in the text), or are described, figured and tabulated
663 within the manuscript or supplementary information of this article.

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Table 1: The species in the Celtic Sea mizer model

<i>i</i>	Common name	Latin name
1	Atlantic herring	<i>Clupea harengus</i>
2	European sprat	<i>Sprattus sprattus</i>
3	Atlantic cod	<i>Gadus morhua</i>
4	Haddock	<i>Melanogrammus aeglefinus</i>
5	Whiting	<i>Merlangius merlangus</i>
6	Blue whiting	<i>Micromesistius poutassou</i>
7	Norway pout	<i>Trisopterus esmarkii</i>
8	Poor cod	<i>Trisopterus minutus</i>
9	European hake	<i>Merluccius merluccius</i>
10	Monkfish	<i>Lophius piscatorius</i>
11	Atlantic horse mackerel	<i>Trachurus trachurus</i>
12	Atlantic mackerel	<i>Scomber scombrus</i>
13	Common dab	<i>Limanda limanda</i>
14	European Plaice	<i>Pleuronectes platessa</i>
15	Megrim	<i>Lepidorhombus whiffiagonis</i>
16	Common sole	<i>Solea solea</i>
17	Boarfish	<i>Capros aper</i>

Table 2: The uncertain parameters.

Parameters	Dimensions	Units	Prior	Notes
$\ln R_{max,1:17}$	17	$\ln(vol^{-1}grams^{-1}year^{-1})$	$U(0, 50)$	Natural log of the maximum recruitment for each species
$\ln \kappa$	1	$\ln(grams^{-\lambda-1}vol^{-1})$	$U(0, 40)$	Natural log of the carrying capacity of the resource spectrum
$\phi_{0,1:17}$	17	$year^{-1}$	$U(0, 1.5)$	The fishing rates during the spin-up period for each species
$\phi_{1:24,1:17}$	$17 \times 24 = 408$	$year^{-1}$	$U(0, 1.5)$	The fishing rate for each species for each year
$\sigma_{s,1:17}^2$	17	Unitless	$Inv - Gamma(2, 2)$	The variance of the error on the natural log survey catches
$\sigma_{c,1:17}^2$	17	Unitless	$Inv - Gamma(0.1, 0.1)$	The variance of the error on the natural log commercial catches

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- 1 A directed acyclic graph of the state-space model. ϕ_t is the dynamical inputs; the fishing mortality values for each species at time t ; M_t is the process model state, the density, in numbers, of all species and the background resource at all weights at time t in the size-based multi-species model; w_t are observations of commercial catches and z_t are observations from the International Bottom Trawl Survey at time t 46
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966	4	The median value of the fishing rates (solid black line),	
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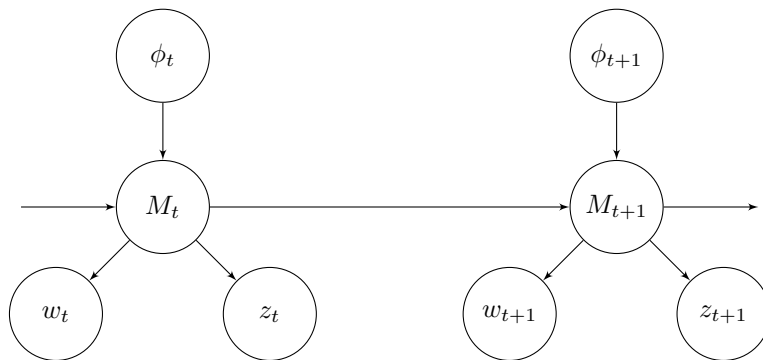


Figure 1: A directed acyclic graph of the state-space model. ϕ_t is the dynamical inputs; the fishing mortality values for each species at time t ; M_t is the process model state, the density, in numbers, of all species and the background resource at all weights at time t in the size-based multi-species model; w_t are observations of commercial catches and z_t are observations from the International Bottom Trawl Survey at time t .

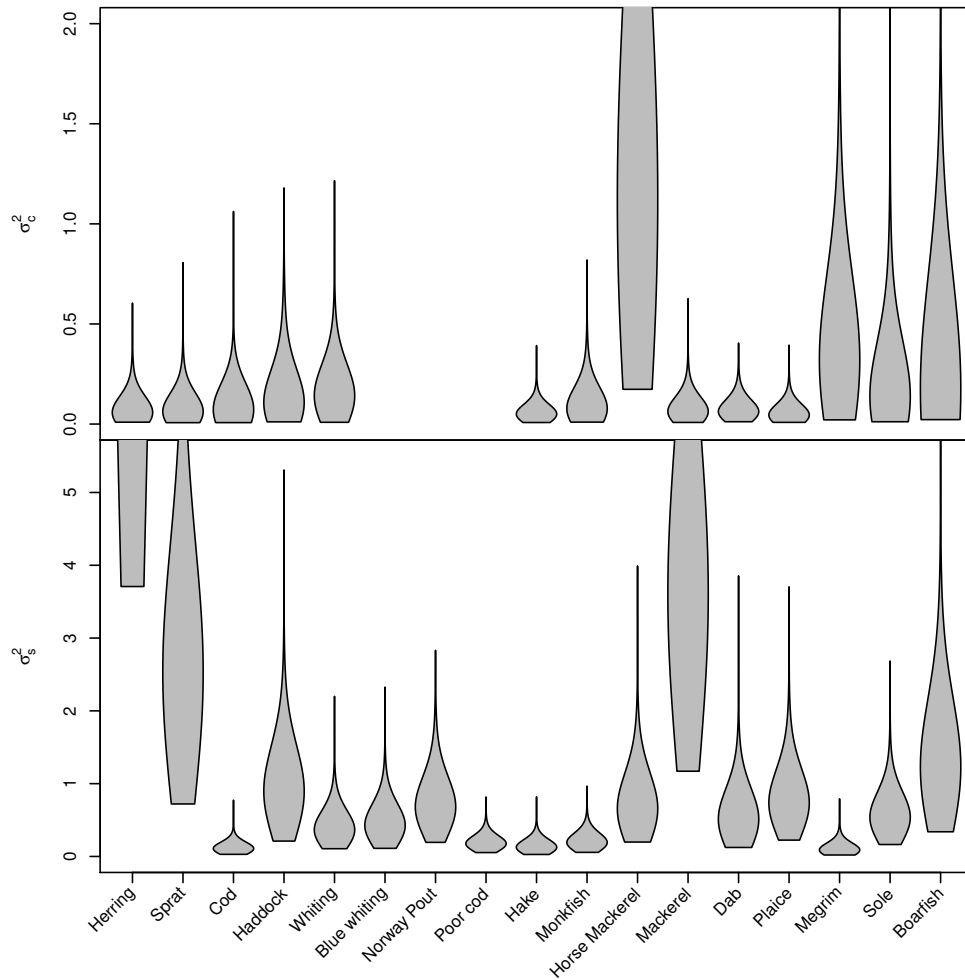


Figure 2: Violin plots showing the marginal posterior distribution for the variance parameters. The top plot shows the variance associated with the catch and the bottom shows the variance associated with the survey. Blue whiting's variance term for the catch was large and therefore was omitted from the plot. In the top plot, we fixed $\sigma_c = 2$ for Norway Pout and poor cod so they have been omitted from the results.

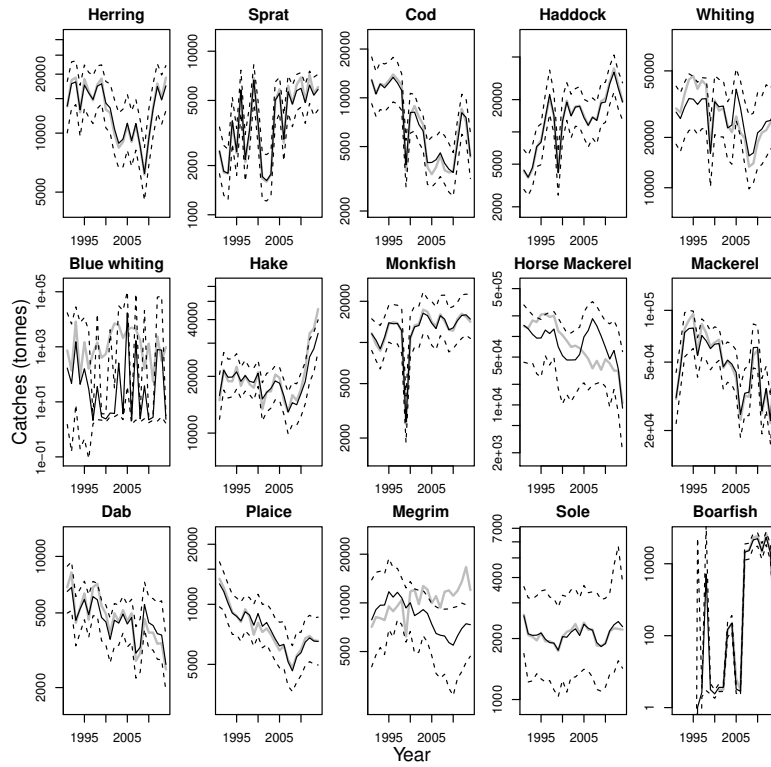


Figure 3: The median modelled commercial catches (solid black line), the 10th and 90th percentiles (dotted black lines) and the observed catches (grey line) for 15 of the 17 species. Norway pout and poor cod have been omitted as the model was not fitted to their landings. The downward spike in landings in 1999 for cod, haddock, whiting and monkfish was caused by the French not reporting landing of these stocks in that year in the dataset (ICES, 2017c).

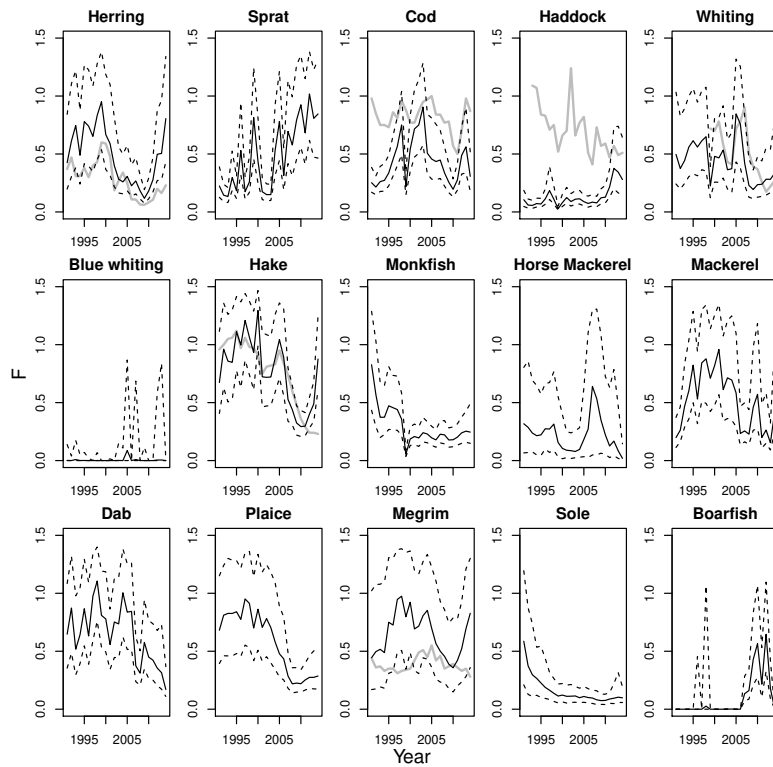


Figure 4: The median value of the fishing rates (solid black line), and the 10 and 90 percentiles, (dotted black lines) for 15 of the 17 species. Norway pout and poor cod have been omitted as the model was not fitted to their landings.

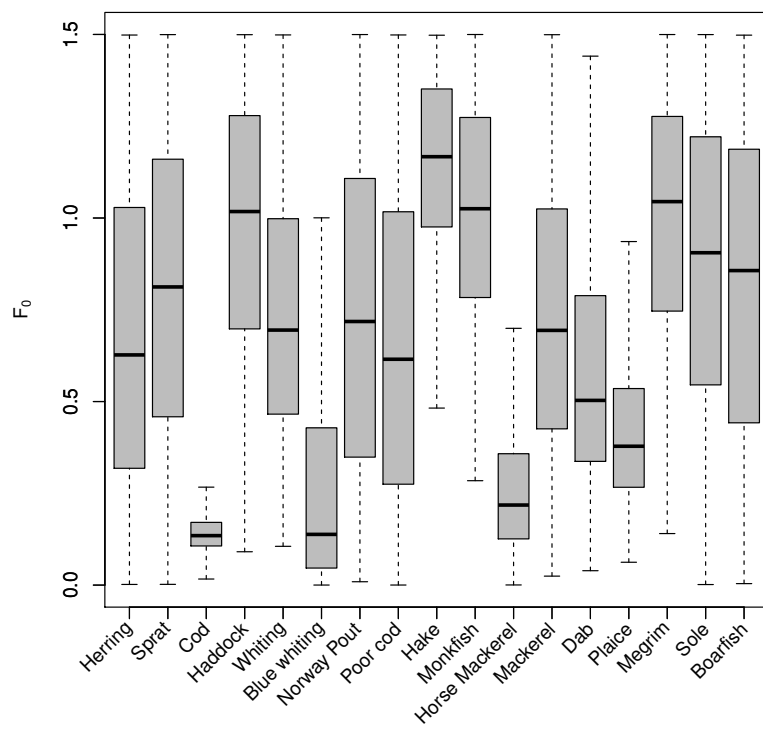


Figure 5: The marginal posterior distributions of the fishing rate during the spin-up period, ϕ_0 .

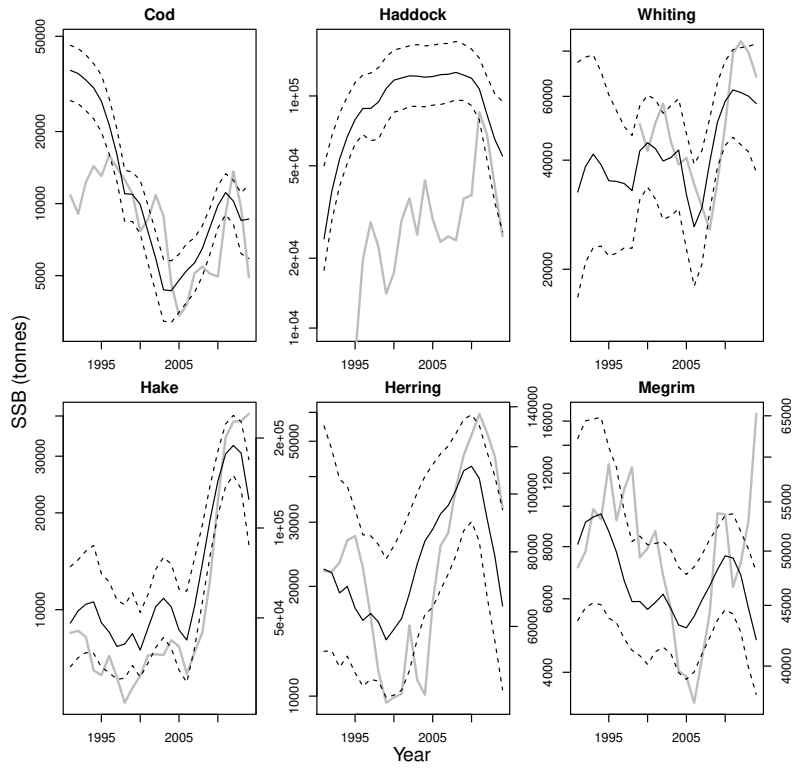


Figure 6: The median modelled SSB (solid black line), the 10 and 90 percentiles (dotted black lines) and SSB estimates from single-species ICES assessments for cod, haddock, whiting hake, megrim and herring (grey line). The hake, megrim and herring assessments cover more area than the model does and therefore is plotted on a different scale.