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1 **Technical Note: Bayesian Fitting of Probabilistic**
2 **Maturation Reaction Norms to Population-level**
3 **Data**

4 Bruce J. McAdam (Corresponding Author)¹

5 C. Tara Marshall²

6
7 ¹ Institute of Aquaculture

8 The University of Stirling

9 Stirling, UK, FK9 4LA

10 +44 (0)1786 46 7891

11 b.j.mcadam@stir.ac.uk

12
13 ² School of Biological Sciences

14 The University of Aberdeen

15 Zoology Building, Tillydrone Avenue, Aberdeen, UK, AB24 2TZ

16
17 Running title: Fitting PMRNs to Population-level Data

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20

21 **Abstract**

22 Probabilistic maturation reaction norms (PMRNs) are an important tool for studying
23 fisheries-induced evolution and environmental effects on life history. To date there
24 has been no way to fit a PMRN to population-level fisheries data; instead individual-
25 level data must be used. This limits the stocks and time periods that can be studied.

26

27 We introduce a Bayesian method for fitting PMRNs to population-level data. The
28 method is verified against both an existing result and simulated data, and applied to
29 historical Barents Sea cod data which combines observations of population-level
30 variation in age, size and maturity status from Russia and Norway.

31

32 The method shows a clear and rapid trend towards greater probability of maturation at
33 smaller lengths in the Barents Sea cod.

34

35 The new model fitting algorithm allows us to study historic changes in life history
36 despite the lack of individual-level data seen in much long term data. Access to more
37 data will aid the study of evolutionary hypotheses in a wide range of organisms.

38 **1. Introduction**

39 Quantifying life history variables as reaction norms is critical to proper management
40 because it affects stock assessment. Especially, expressing maturity as a function of
41 size and age (the probabilistic maturation reaction norm, PMRN, Heino et al 2002b)
42 has proven valuable in accounting for demographic effects on the maturity ogive, and
43 in diagnosing fisheries induced evolution towards earlier maturation (see, for
44 example, Heino et al 2002a, Heino et al 2002c, Grift et al 2003, Olsen et al 2004,
45 Kuparinen and Merilä 2007).

46

47 A range of techniques for fitting PMRNs to different types of data are available,
48 following a gradient from those requiring specialized data (Heino et al. 2002b) to
49 those dealing with data collected routinely for other purposes (Barot et al. 2004a,
50 Scott and Heikkonen 2012). Heino et al (2002b) constructed PMRNs for a cohort
51 using logistic regression on age and size data from two sub-components of the cohort:

52 those individuals who matured in the past year and individuals who are immature
53 (individuals that matured in previous years are irrelevant to the calculation). This
54 type of data will be available if animals are studied through their lives in laboratory
55 experiments, and can sometimes be extrapolated from scale-ring or otolith studies of
56 wild fish. Long-term databases describing maturation in commercial fish stocks
57 typically lack sufficient resolution to specify the exact age and size that the
58 individuals became mature. To circumvent this problem, variations on the original
59 model fitting approach have been developed. Heino et al (2002a) dealt with data sets
60 that describe the sizes and ages of maturing fish (those that matured in the past year),
61 but lack information on immature fish. Data of this form can occur if sampling omits
62 immature fish, for example if they have a different spatial distribution. The method
63 first back-projects the sizes of immature fish using independently obtained maturity
64 ogives, and then uses logistic regression on the resultant data set. Barot et al (2004a)
65 examined data sets in which maturing fish are not distinguished from mature fish (that
66 matured more than a year ago). This form of data is typically obtained during surveys
67 or by sampling commercial catches. The method first constructs a size- and age-
68 based maturity ogive and from this extrapolates the proportion of fish maturing at
69 each size and age, finally logistic regression is applied to yield a PMRN. These
70 techniques have led to a proliferation of studies applying the PMRN approach to
71 commercial stocks and the majority have found results consistent with FIE
72 (Dieckmann and Heino 2007). These existing methods share the common
73 requirement of individual-level data about size, age and maturity status. There
74 remains a wealth of data, much of it associated with routine surveys (e.g. DATRAS
75 database <http://datras.ices.dk/>), that could produce insights into FIE but are not
76 amenable to individual-level methods.

77
78 This paper aims to complement the existing repertoire of tools by providing a
79 Bayesian method based on simulation of growth and maturation, to be used when
80 such traits are described at a population-level only. Such data can arise if different
81 variables are measured on different individuals during different surveys. We
82 demonstrate the new method by testing whether there is evidence for FIE in Northeast
83 Arctic (NEA) cod *Gadus morhua* using a long term database (1946—1989 cohorts).
84 The data were obtained from both Norwegian and Russian sources. The database
85 covers a larger geographical extent than previous PMRN studies of the stock (Heino

86 et al. 2002c, Heino et al. 2002a). For much of the period of interest, individual-level
87 data are not available from Russian sources which necessitates a method that can be
88 applied to population-level data. The method is also validated against an independent
89 existing result obtained by Grift et al (2003) for North Sea plaice, and a synthetic data
90 set based on the NEA cod.

91 **2. Theory and Calculation**

92 **2.1 Probabilistic Maturation Reaction Norms**

93 Mathematically, a PMRN is a function taking a description of fish state as arguments,
94 and returning the probability that the fish will have matured within the last year.

95 Typically, probability follows a logistic relation to size with different coefficients for
96 every age of fish as in eqn 1:

97

$$98 \text{logit}(p(a, s)) = c_{a,1} + c_{a,2} s \quad (1)$$

99

100 where $p(a, s)$ is the probability that a previously immature fish of age a and size s will
101 have matured in the last year. An example using results about North Sea plaice in
102 Grift et al (2003) is shown in Figure 1. The model is represented by contours of
103 constant probability of maturation. If a plaice is 30cm at age 3 then it will have
104 approximately 25% chance of having matured; if it does not mature at age 3 and
105 grows to 35cm by age 4 then it will have a 50% probability of maturing. The
106 probability of a fish being mature is the cumulative probability of maturing at each
107 annual point on its growth curve. In this case, there is a 62.5% probability of
108 maturing by age 4.

109

110 Variants of the model use different functions of s and a . Most models (e.g. in Figure
111 1) have distinct coefficients for each age of fish. Coefficients for each age in these
112 models are fitted using data on the fraction maturing only from that age. In this paper,
113 however, data from all ages is used to fit a smaller number of coefficients which apply
114 to all ages. Specifically, we use models with linear coefficients of age, so contours
115 are straight parallel lines

116

$$117 \text{logit}(p(a, s)) = c_1 a + c_2 s + c_3 \quad (2)$$

118

119 Linear models are chosen as a convenient approximation of the true shape of PMRNs.
120 Theoretical and laboratory-based work (Stearns and Crandall 1984, Stearns and
121 Koella 1986, Reznick 1990, Ernande et al. 2004, Plaistow et al. 2004) suggests that
122 contours should be L-shaped curves, so that there is low (or zero) probability of
123 maturity when very young, regardless of size. Existing work on NEA cod (Heino et
124 al. 2002c, Heino et al. 2002a) suggests that this stock has contours with a slight dome
125 and overall upward gradient. Linear models are chosen for this study because they
126 have only three parameters to estimate and because they roughly approximate both the
127 asymptote of an L-shaped curve or a shallow curve as depicted in Figure 1.

128 **2.2 Bayesian Analysis**

129 Existing logistic-regression-based methods for fitting PMRNs cannot be used with the
130 combined Russian-Norwegian Barents Sea cod data set because it lacks individual-
131 level information relating size to maturity status. The data available, instead, consist
132 of length distribution at each age and fraction mature at each age, for every cohort. In
133 our Bayesian method model parameters are drawn from prior distributions and
134 assigned an estimate of likelihood by repeatedly simulating observations of the
135 maturity status of fish and recording the fraction of simulations that match the actual
136 observations (which estimates $P(\text{observations} \mid \text{parameters})$). Bayes' law then allows
137 these likelihoods to be converted into the posterior distribution of the parameters,
138 $P(\text{parameters} \mid \text{observations})$.

139

140 In the method, each simulated fish is assigned a maturity status according to its length
141 and age. In order to do this, the probability of the fish being mature must be
142 calculated from the probability of becoming mature at each prior age. A PMRN gives
143 the probability, $p(a, s)$, of a fish maturing at age a and length s . The probability of an
144 individual being mature at a and s can be calculated using eqn 3 (based on eqn 2 in
145 (Barot et al. 2004a)).

146

$$147 \quad P(\text{mature} \mid a, s_a) = P(\text{mature} \mid a-1, s_{a-1}) + P(\text{immature} \mid a-1, s_{a-1}) \times p(a, s) \quad (3)$$

$$148 \quad = P(\text{mature} \mid a-1, s_{a-1}) + (1 - P(\text{mature} \mid a-1, s_{a-1})) \times p(a, s)$$

149

150 The equation is derived from the fact that a mature fish was either mature last year, or
 151 was immature last year and matured within the last year. Since all age 0 fish are
 152 considered to have zero probability of being mature, the equation can be used
 153 recursively provided that there is a way of back-calculating s_{a-1} , the length of the fish
 154 the previous year. We use an empirical growth model that assumes each fish
 155 maintains its position within the cohort (e.g. a cod at the 87th percentile of length in its
 156 cohort at age 6 will still be at the 87th percentile at age 7). All simulated lengths are
 157 the midpoint of 5cm length classes. This makes the implicit assumption that the effect
 158 of length on mortality within classes is negligible. Similar assumptions are made in
 159 other methods for fitting PMRNs (Heino et al. 2002a) and any bias in the results
 160 caused by these assumptions will be similar and will not prevent results from this
 161 method being compared with other methods.

162

163 Estimating likelihood for a particular set of model parameters for a single cohort uses
 164 the algorithm in Table 1. The model is a linear probabilistic reaction norm with three
 165 parameters: S_6 , the size for 50% probability of maturation at age 6 (age 6 is chosen as
 166 a typical age to mature, other species may require other ages, this controls the
 167 intercept of the 50% contour, S_0); S' , the slope of the contours; and W , the width
 168 between contours (difference in length between a fish with 25% probability of
 169 maturation, and one with 50% probability). The equation for the model is

170

$$171 \quad \text{logit}(p(a,s)) = \frac{\text{logit}(0.75)}{W}(s - a \times S' - S_0) \quad (4)$$

172

173 Where $S_0 = S_6 - 6S'$ and the sigmoidal logistic function is defined in the usual way

$$174 \quad \text{logit}(p) = \log(p/(1-p)) \quad (5)$$

175 The method simulates the growth of a number, F , of fish of each age class, and is
 176 repeated for a number, R , of replicates. Preliminary trials showed that $F=15$ fish of
 177 each age per simulation and $R=150$ simulations per age class yielded reasonably
 178 consistent probabilities for each model. Larger numbers of replicates improve
 179 accuracy, but greatly reduce the fraction of simulations that match observations and
 180 thus require more simulations and computation time.

181

182 Every tested set of model parameters is drawn independently from the joint prior
183 distribution. There is no chain of estimates converging on a solution as in Markov
184 Chain Monte Carlo (MCMC) methods. This means that there is no need to choose a
185 length of model run or thinning frequency in order to ensure the model has converged
186 and does not suffer from autocorrelation. It also simplifies implementation and makes
187 it easier to run several parallel processes (we used 6 processes, each testing 2000
188 independent parameter sets).

189

190 The parameters for cod were drawn from uniform priors chosen on the basis of
191 existing work on cod (Heino et al. 2002a, Heino et al. 2002b, Barot et al. 2004b, Barot
192 et al. 2004a, Olsen et al. 2004): $0 \leq S_6 \leq 300$ cm, $-20 \leq S' \leq 20$ cm y^{-1} and $10 \leq W \leq 20$
193 cm. The same 12000 sets of parameters were tested for every cohort. This number
194 was chosen as it allowed patterns to be clearly distinguished, without requiring too
195 much computation time. The result of applying our method to the cod data is a
196 posterior distribution for the PMRN parameters. All candidate parameters are
197 assigned relative probabilities, $P(\text{parameters} \mid \text{observations})$, of how likely they are to
198 be correct, given the observations. The probabilities sum to 1 and directly reflect the
199 fraction of all successful replicates for which the model was responsible. Estimates of
200 model parameters and their Bayesian confidence intervals are obtained from the
201 posterior distribution. The maximum likelihood model is the one with greatest
202 $P(\text{model} \mid \text{observations})$.

203

204 **3. Methods and Materials**

205 **3.1 Northeast Arctic cod**

206 Temporal trends in maturation of the NEA cod have been previously analysed using a
207 Norwegian database about the fraction of the stock on spawning grounds around
208 Lofoten from 1932 (Jørgensen 1990). Early applications of PMRNs used both
209 historical data (1926 cohort) and contemporary survey data (1981-1990 cohorts) for
210 NEA cod (Heino et al. 2002c, Heino et al. 2002a), but the individual-level
211 observations were based only on the portion of the stock fished by Norway. To date,
212 there has been no continuous reconstruction of PMRNs that has used both Norwegian
213 and Russian maturity data.

214

215 Our data combines surveys from both Russia and Norway. The data is structured into
216 cohorts (fish spawned in the same year) from 1946--1989 and age classes from 3—13.
217 Older and younger fish are all mature or immature respectively, and do not affect a
218 study of maturation. The data consists of age-based maturity ogives, and age-length
219 keys, illustrated for a single cohort in Figure 2 and described below. These are two
220 types of data commonly available for many commercial fish stocks.

221

222 The maturity ogive (AFWG 2006) records the fraction of fish mature in every age
223 class of every cohort. Maturity data are based on visual examination of ovary state.
224 A mature fish skipping spawning (e.g. due to malnutrition) may appear to be
225 immature. Because of this, the proportion of mature fish in some cohorts appears to
226 decline from one age to the next. Similar artefacts can be caused by sampling error or
227 increased mortality of mature fish. Such problems are likely to be typical of other
228 data sets and no attempt has been made to correct for these errors before fitting the
229 models.

230

231 The age-length keys (ALKs) partition the fish into 5cm length classes (Marshall et al.
232 2004). For every cohort-age-length class the ALK records the fraction of fish from
233 the cohort-age class that were that length. Because of sampling artefacts, some
234 cohorts have some smaller fish in older age classes than in younger ones; again no
235 attempt is made to correct the data prior to model fitting. When combined, the ALK
236 and maturity ogive do not reveal the different sizes of mature and immature fish, and
237 do not give information about any individual.

238 **3.2 Validating simulation-based method with North Sea plaice data**

239 In order to validate the algorithm, data were obtained to which an existing method
240 (Barot et al 2002) had been applied. These data described two cohorts of female
241 North Sea plaice from Grift et al (2003). These data were chosen to provide a test
242 completely independent of the NEA cod, and for which previous results have been
243 published. The data contained age, length, and maturity status of individual fish. In
244 total, there were 45 observations of fish from the 1960 cohort, and 264 from 1990.
245 Observations were made of fish from ages 2 to 6 years. Sampling was based on
246 market size categories (lengths ranged from 25.2 to 52.1cm) so the lengths of

247 observed fish are not representative of the population. The data were summarised to
248 a form analogous to the NEA cod data: fraction of mature fish of each sampled
249 cohort-age group; and cohort, age and length of each observed fish. The information
250 relating maturity status to length was discarded (to make it comparable with the NEA
251 cod data in which this was not present).

252

253 The plaice data differs from the cod data because the sampled fish are not
254 representative (with respect to length) of the population. This means that a different
255 method is required to back-calculate the length of observed fish in the previous year,
256 s_{a-1} . Grift et al (2003) used otolith measurements to calculate the change in length
257 each year, but we did not have access to this data. Instead, we obtained an ALK for
258 North Sea plaice (WGSSDS 2006). This gave the mean and standard-deviation of
259 length for each cohort-age class ($\hat{s}_{c,a}$ and $\sigma_{c,a}$, respectively). The length of a fish at
260 age a can be expressed as $s_a = \hat{s}_{c,a} + k \times \sigma_{c,a}$. Assuming that the coefficient k is
261 constant throughout the fish's life (i.e. the fish maintains its position in the population,
262 as in the cod case), the length in the previous year is $s_{a-1} = \hat{s}_{c,a-1} + k \times \sigma_{c,a-1}$.

263

264 There was a slight difference in the procedure used to calculate likelihood. This was
265 because the precise number of mature plaice out of a is known (rather than the
266 fraction mature in a sample of unknown size). For this reason, each replicate for the
267 plaice data consists of fish of exactly the lengths sampled, rather than drawing lengths
268 randomly from the age ALK (i.e. the loop on line 5 of the algorithm in Table 2 is “for
269 every actual length sampled”). The number of fish in each replicate varied between 2
270 and 24. As larger replicates have a lower probability of success, the number of
271 replicates, r , was raised to 200 (from 150 for the cod). 12000 linear models were
272 tested, with parameters drawn from uniform priors such that $0 \leq S_4 \leq 60$, $-7 \leq S' \leq 7$
273 and $0 \leq W \leq 15$, based on the maximum length of plaice (52.1cm in the data set).

274 **3.3 Validating Fitting of PMRN Slope**

275 Initial investigation of the method led to concern that it could not distinguish correctly
276 between different slopes of PMRN, in particular that it was biased towards selecting
277 steep negative slopes. This is a particular concern for NEA cod as previous research
278 has found an overall slight positive slope (9cm over 5 years from Fig 5c of Heino et

279 al. (2002c)). In order to test whether bias exists, two example linear PMRNs with
280 parameters $S_6=100$, $S'=4$, $W=15$ (positive slope) and $S_6=100$, $S'=-4$, $W=15$ (negative
281 slope) were selected. Synthetic maturity ogives were created by simulating the
282 maturation of a cohort of cod following the 1980 cohort ALK and each of the two
283 selected PMRNs. The model fitting method for cod was applied to the actual 1980
284 ALK and each synthetic maturity ogive.

285 **4. Results**

286 **4.1 North East Arctic Cod**

287
288 Figure 3 shows both (a) the single best model found for the 1980 cohort, and (b) the
289 models that accounted for 95% of all successful replicates (the 95% Bayesian
290 confidence interval of the posterior). Figure 3a is the usual presentation of PMRNs
291 (as in Figure 1), 3b allows visualisation of the uncertainties in model fitting. It can be
292 seen that as the cod grow through the contours of the PMRN, maturity rises.

293 Furthermore, the fraction mature starts to rise when the largest fish are reaching the
294 25% probability of maturation contour, and most of the fish are mature once they lie
295 in the region between 25% and 75% of maturation. It can also be seen that the
296 uncertainty is greater in regions for which there is little data, e.g. all age 12 fish are
297 mature, so there is no information about where the 50% contour should be at age 12.

298
299 Figure 4 shows the parameter space for the PMRNs, parameters that were tested, and
300 parameters that matched four cohorts through the time series. Several features are of
301 interest. Firstly, S_6 and S' are correlated. Secondly the correlation between S_6 and S'
302 accounts for most of the within cohort variation in parameter estimates. Thirdly, the
303 cohorts shown have very little overlap in the joint model parameters. This means that
304 the maturation reaction norms for these cohorts are quantitatively distinct. In
305 addition, there is a trend in the parameters over time corresponding to smaller size at
306 maturation between 1946 and 1974. Figure 5 shows the PMRNs for the same cohorts
307 in detail. The trend towards maturation at smaller sizes is seen from the fact that the
308 contours for later cohorts are lower on the graph than for earlier cohorts. From 1974
309 to 1989, the change is in the slope of the contours, with the 1974 fish having steeper

310 contours and, hence, a more sudden rise in maturity with age as seen in the inset
311 maturity graph.

312

313

314 To summarise changes in maturation patterns over time by focusing on a single age
315 class Figure 6 shows the length a 6 year old fish born in each year would have to be to
316 have a 50% chance of maturing and can be regarded as a summary of the effect of all
317 the model parameters. It shows an irregular decline in length. Note that although the
318 graph is for 6 year old fish, it is based on models derived using all age classes.
319 Similar patterns are seen with other age classes, in particular the dip between 1972
320 and 1976 is always present.

321

322 The rate of phenotypic change can be measured from Figure 6. Taking the trait as
323 size for 50% probability of maturation at age 6, gives -12 000 darwins (relative
324 change per million years) or -0.68 haldanes (standard deviations of change per
325 generation). Values were obtained using weighted linear regression on point
326 estimates produced by the tested parameters weighted by posterior probability.

327

328 **4.2 Validation of method**

329 Figure 7 shows that the linear PMRNs from the simulation-based method are a
330 reasonable approximation of the curves obtained for decade-long periods including
331 1955—1964 and 1985—1994 by Grift et al (2003) using the method in Barot et al
332 (2004a). The fit has clear differences (especially for 1990), but this is to be expected
333 for two reasons. Firstly, the model fit using our method is based on slightly different
334 data (a single cohort, rather than a decade of cohorts). Secondly, the original model
335 fitting was not restricted to linear models, so an exact match between methods is not
336 possible.

337

338 Results of fitting PMRNs to synthesised maturity ogives created with different sloped
339 linear PMRNs are shown in Figure 8. When the real slope of the PMRN is negative,
340 then the model fitting performs well (Figures 8a and 8c). When the real slope of the
341 PMRN is positive, then the model fitting selects slopes that are smaller than the actual

342 slope or more negative (Figures 8b and 8c). These show bias towards negative slopes,
343 but that it can distinguish between maturity ogives generated by differently sloped
344 PMRNs (the “A” and “B” marks in Figure 8c are non-overlapping). Hence, the
345 method makes the correct qualitative comparison between the cohorts even if the
346 values are not precisely estimated.

347

348 The model fitting shows that a more negative slope must have a higher intercept
349 (correlation between S' and S_0 in Figure 8c). There is a clear geometric reason for this
350 correlation, as steeper slopes passing through the same region will necessarily have
351 higher intercepts. In models like this, the probability of maturation is determined
352 more by age than size. The model fitting is biased to select models like this as the
353 data only provides indirect evidence of the influence of size on maturation. The use
354 of priors for model parameters excludes biologically unrealistically steep slopes.

355 **5. Discussion**

356 The analyses described in this paper are informative both from a methodological point
357 of view in assessing the new algorithm and the PMRN approach, and an ecological
358 point of view in revealing patterns in the biology of the cod stock. The method opens
359 up the possibility of studying maturation trends in many more fish stocks and other
360 organisms with suitable population-level data. The results suggest some limitations
361 and possible refinements of the technique. First the effectiveness of the algorithm is
362 discussed, as all other discussion rests upon this.

363 **5.1 Data Analysis**

364 Comparison with Grift et al's (2003) results and testing against synthetic data show
365 that the method has a slight tendency to overestimate the downward slope of the
366 PMRN contours, meaning that the effect of age on maturation is overestimated. This
367 can be controlled by choosing appropriate prior distributions for the model
368 parameters. For most commercial fish species, existing work on maturation will
369 suggest values for these priors, although in the case of suspected FIE it is important to
370 choose conservative priors and to use the same priors for all time periods to prevent
371 the prior from biasing results. Even when models produced by the new method differ
372 from other methods, the trends in maturation that they show are the same. As it is the
373 presence of a trend that is typically of interest, rather than the precise model

374 parameters, the new method is equally suited to testing for a change in maturation
375 dynamics.

376

377 We conclude that the method is effective at fitting PMRNs because the new method
378 shows the same qualitative differences between cohorts as the original analysis and
379 allows the same conclusion regarding FIE to be drawn.

380

381 Bayesian methods typically use MCMC methods to overcome the problem of large
382 parameter spaces to search and to focus search on the resulting posterior distribution
383 rather than the (much more dispersed) prior parameter distribution. In the case of
384 these PMRN models, there are few parameters and the prior distribution is relatively
385 constrained (because it can be linked to well known features such as the size of the
386 fish). This meant that it was not necessary to use MCMC methods, but just to
387 perform a brute-force search of the prior parameter space. This avoids several
388 problems with MCMC methods: they are somewhat more complex to implement as a
389 computer program; and the modeller must ensure that the chain length is sufficiently
390 long to ensure convergence, enough of the initial run-in period is discarded, and the
391 chain is ‘thinned’ sufficiently to avoid autocorrelation. It was also easy to take
392 advantage of the multiple processors found on modern desktop computers by running
393 several separate processes each testing a different set of model parameters.

394

395 We fitted models that used S_6 (cod) or S_3 (plaice) as parameters for the intercept of the
396 PMRN contours. Qualitatively similar results were obtained using S_0 (results not
397 shown) but as this is not biologically meaningful (there is zero chance of an age 0 fish
398 maturing at any viable size), and it increases the correlation between the intercept
399 parameter and slope, we favour the approach of using the intercept at an older age.

400 **5.2 Northeast Arctic Cod**

401 The analysis of Northeast Arctic cod data reveals a long trend of decline in size at
402 maturation. The trend is rapid and comparable with other studies of cod (Olsen et al.
403 2004) including this stock (Heino et al. 2002c, Heino et al. 2002b). The rate of
404 change, measured in either darwins or haldanes, is close to the fastest rates cited by
405 Hendry and Kinnison (1999) but less than the maximum rates measured by Devine et
406 al 2012. Rates of these magnitudes have only been seen in phenotypic studies of

407 organisms over very short periods of time (e.g. change in colour spots of guppies
408 *Poecilia reticulata* measured over three generations by Endler (1980)). The rapidity
409 of the change suggests that evolution may not be the sole cause. The time series in
410 Figure 6 also shows a possible discontinuity in the late 1970s and other evidence in
411 the form of weight-length-maturity relationships supports this notion of a shift
412 between two time periods for this stock (Marshall and McAdam 2007), other aspects
413 of stock dynamics also shifted abruptly for these cohorts (Marshall et al. 2006). For
414 this particular stock, we hypothesise that longterm changes in the prey availability or
415 temperature (Yndestad 2003) may have altered maturation in a way that age-and-
416 length-based PMRNs cannot account for. Although this study shows a clear
417 phenotypic change, like other PMRN-based studies, it is not capable of conclusively
418 establishing whether this is a result of plasticity or evolution.

419 **5.3 Broader application of Bayesian Methods**

420 We have shown that a Bayesian method based on simulation can be used to model one
421 aspect of a fish stock's life history, even though the data are not suitable for analysis
422 with other methods. It is likely that similar methods can be found for other aspects of
423 life history such as growth and fecundity, and other examples such as Scott and
424 Heikkonen's (2012) method for fitting PMRNs based on inflection points in growth
425 curves already exist for particular forms of data. There is increasing concern about
426 climate change and prolonged high levels of fishing mortality impacting on the life
427 history of our fish stocks (e.g. see Law and Grey 1989, Law 2000, Stokes and Law
428 2000, Conover and Munch 2002, Kenchington et al 2003, Jorgensen et al 2007), but
429 with the wealth of historic data available on fisheries, we are hopeful that new
430 analytic methods can be used to give a clearer long-term view of the state of our
431 fisheries.

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563 Table 1: Simulation-based algorithm for finding likelihood $P(\text{observations} |$
 564 parameters) where the model is a probabilistic reaction norm, $p(a, s)$, parametrised by
 565 intercept, S_0 , slope, S' , and width, W , and the observations are a single cohort of cod
 566 data consisting of length distribution at age and age based ogive (fraction mature at
 567 age $\{m_a | a_{\text{recruit}} \leq a \leq a_{\text{max}}\}$).

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- 569 1. For each age class, a , $a_{\text{recruit}} \leq a \leq a_{\text{max}}$
- 570 2. Repeat R replicates for this age, recording number that are successful
- 571 3. Expected number of mature fish comes from m_a in the ogive $F_{\text{exp}} =$
 572 $\text{round}(F m_a)$
- 573 4. Draw F fish lengths, $\{s_i | 0 \leq i < F\}$ from the length distribution for
 574 age a
- 575 5. For each of these F simulated fish
- 576 6. Calculate probability $P(\text{mature} / a, s_i)$ of this fish being
 577 mature using back-calculating lengths for earlier ages (eqn 3)
- 578 7. Assign the fish a maturity status according to a single Bernoulli
 579 trial with $P(\text{mature} / a, s_i)$
- 580 8. If the fish is mature, then increment count F_{sim} of mature fish at
 581 this age
- 582 9. If $F_{\text{sim}} = F_{\text{exp}}$ then this trial is successful at age a
- 583 10. Likelihood at this age, $P(\text{observations} | S_0, S', W)$, is fraction of the R
 584 replicates that were successful
- 585 11. Likelihood over all ages is the product of the likelihood for each age,
 586 $P(\text{observations} | S_0, S', W) = \text{PROD}(\text{FOR ALL } a)(P(\text{observations} | S_0, S', W))$

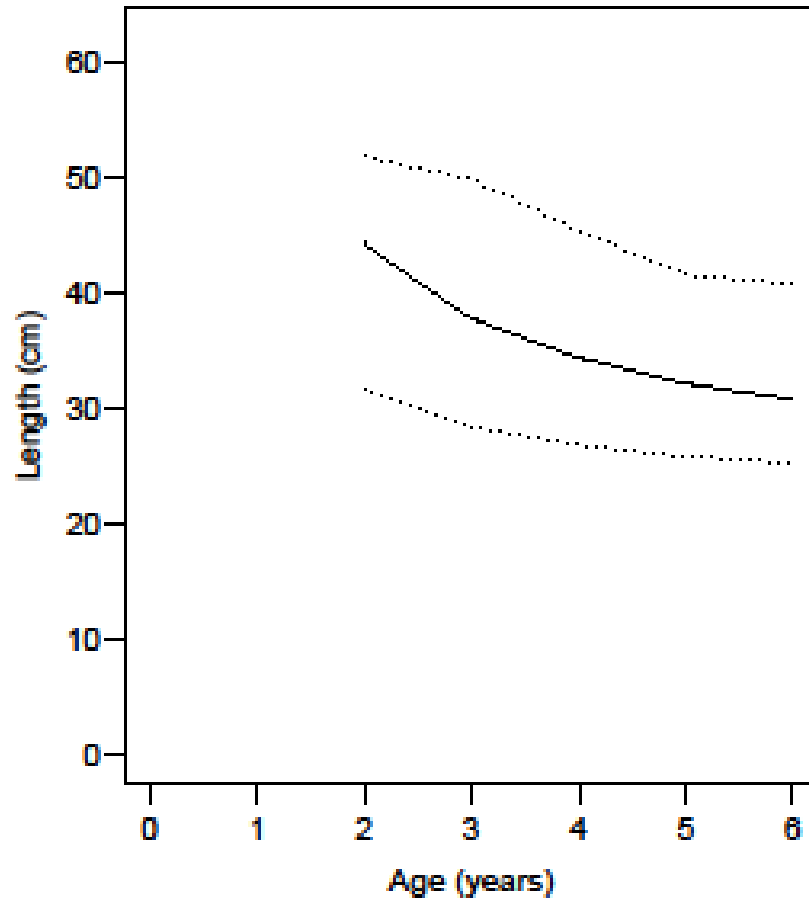
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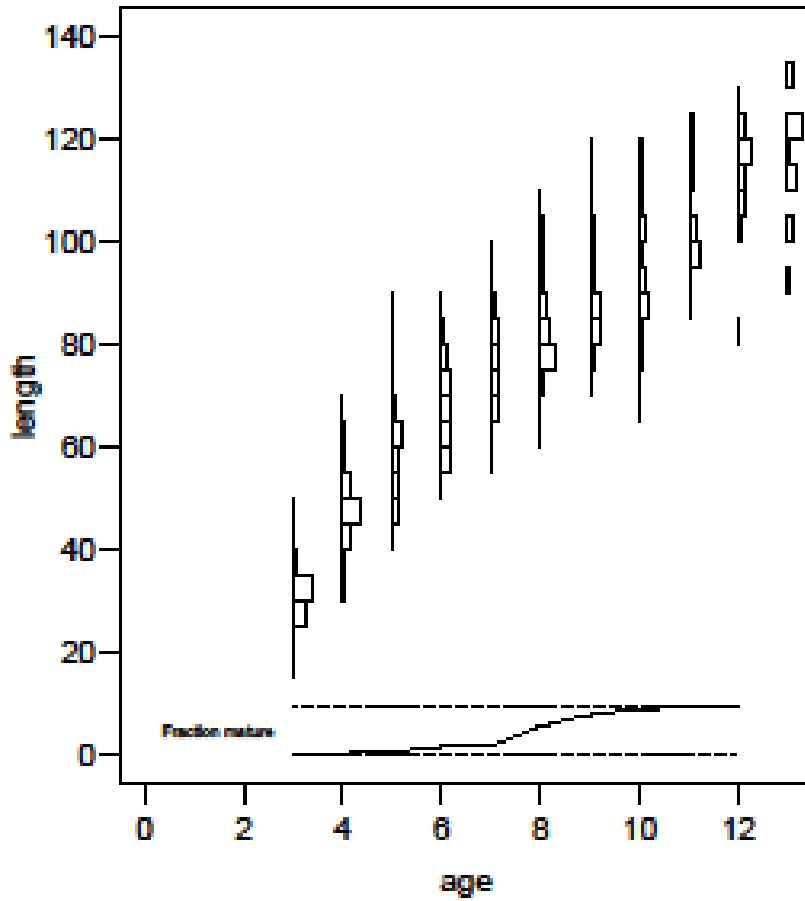
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591 Figure 1: PMRNs for North Sea plaice 1955-1964 cohorts (redrawn from values in
592 Grift et al (2003)). Solid line is 50% probability of maturation; dotted lines are 25%
593 and 75%.



594 Figure 2: All data about the 1980 NEA cod cohort. Boxes show the fraction of each
595 age-class that is within each 5cm size class. The graph at the bottom shows how the
596 fraction of fish mature varies with age from 0 to 100% (limits marked with horizontal
597 dotted lines).

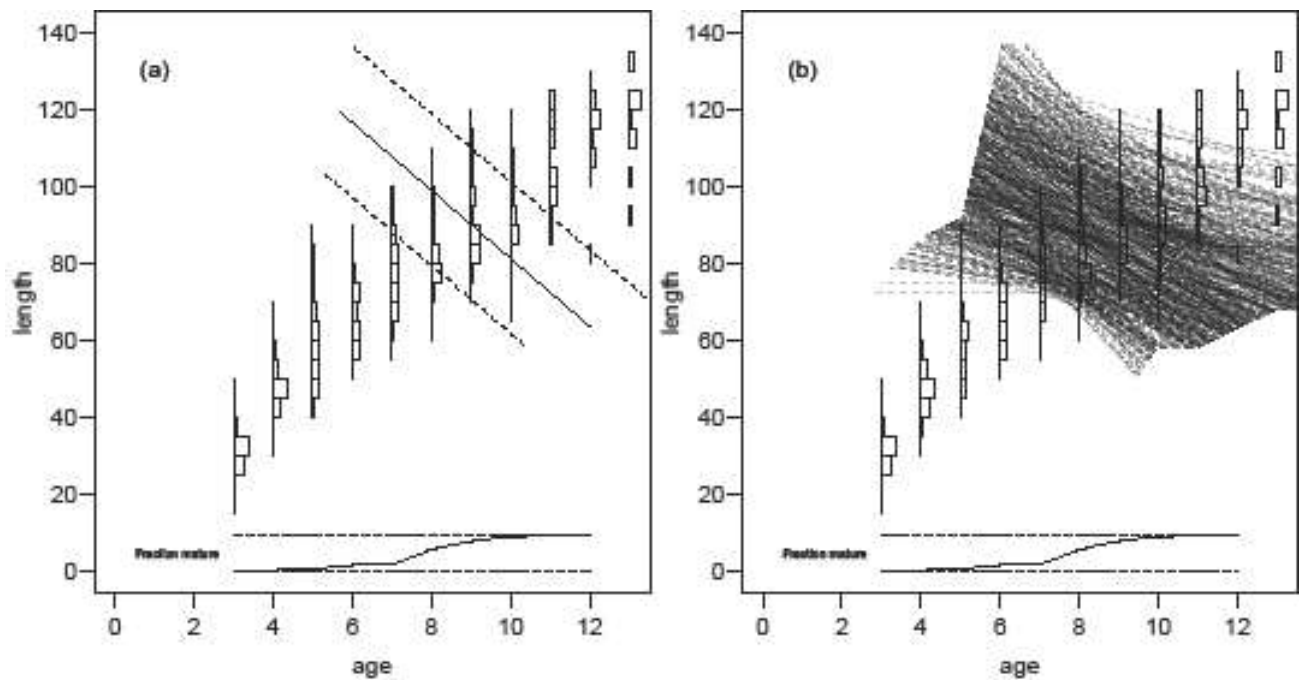


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599 Figure 3: NEA cod. (a) Single best model, and (b) 95% bayesian confidence interval
600 for 1980 cohort (the models that accounted for 95% of all matches between a
601 simulation and observations, line density indicative of posterior probability). Solid
602 lines are the 50% probability of maturation contour. Dotted lines are 25% and 75%
603 probability. Lines are cropped to cover only age-length combinations of NEA cod
604 that have been observed. Other features as Figure 2.

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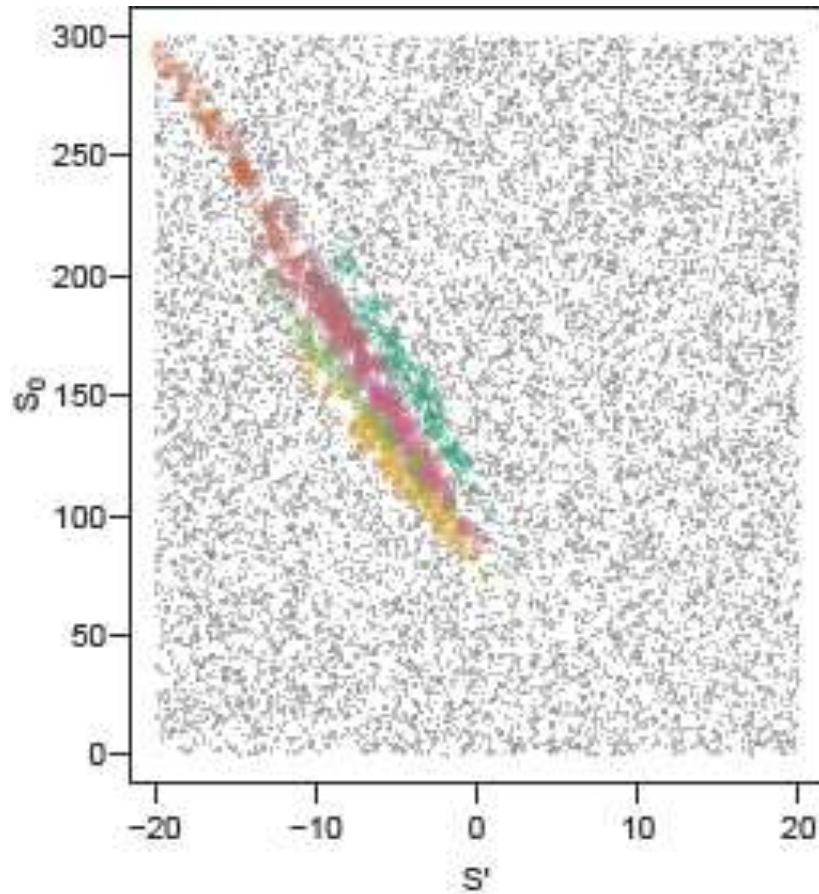
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618 Figure 4: Parameter space for PMRNs for NEA cod, and results for four evenly-
619 spaced cohorts. Grey dots are tested models, letters indicate the 95% Bayesian
620 confidence interval for each cohort, A 1946, B 1960, C 1974, D 1989.

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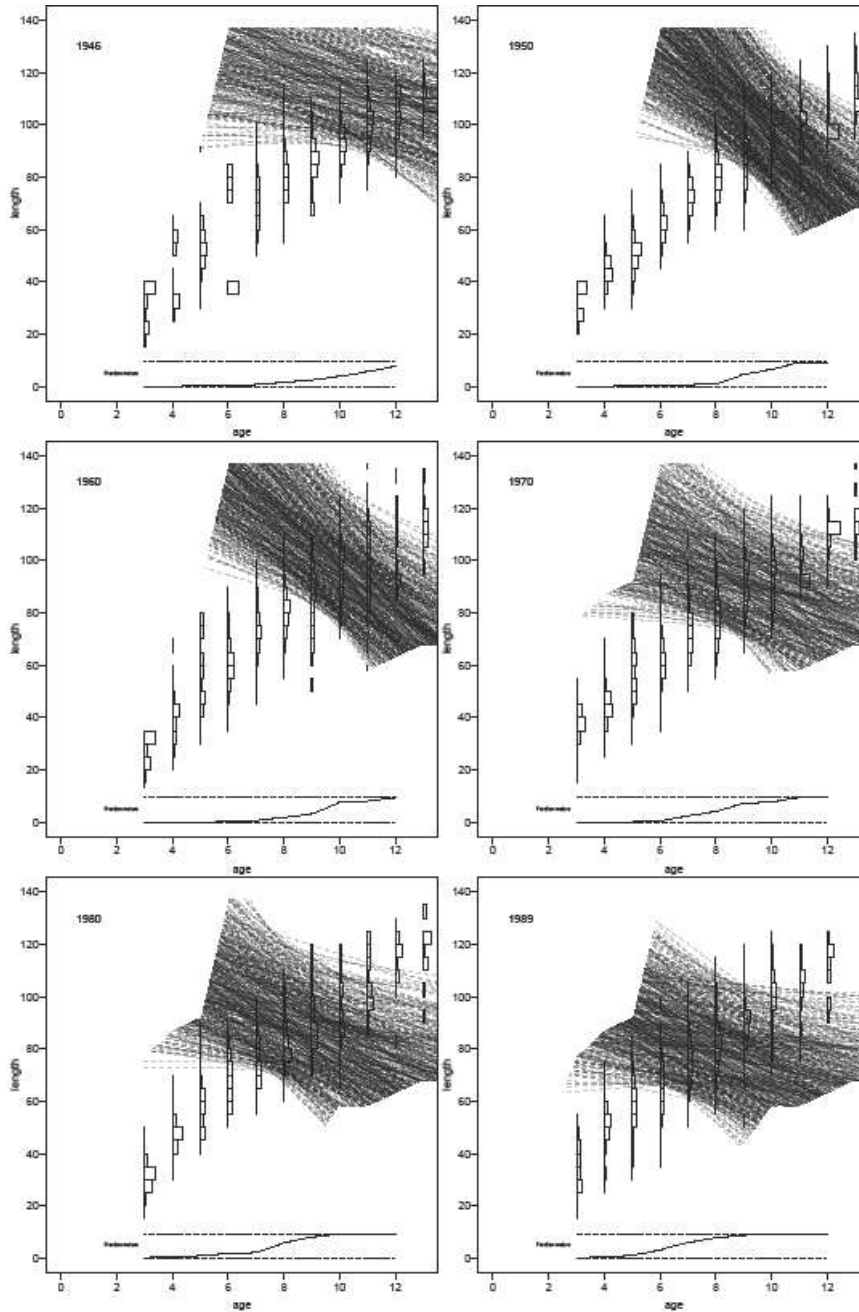
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635 Figure 5: Plots of the PMRNs from Figure 4 (a) 1946, (b) 1960, (c) 1974, (d) 1989.

636 Presentation as in Figure 3b.

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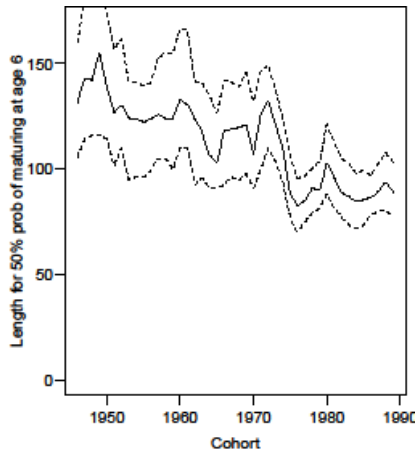
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645 Figure 6: Size at which a 6 year old NEA cod has a 50% probability of maturing for
646 each cohort. Values were sampled from the models according to their posterior
647 probability to obtain median (solid line) and 95% confidence intervals (dotted lines).

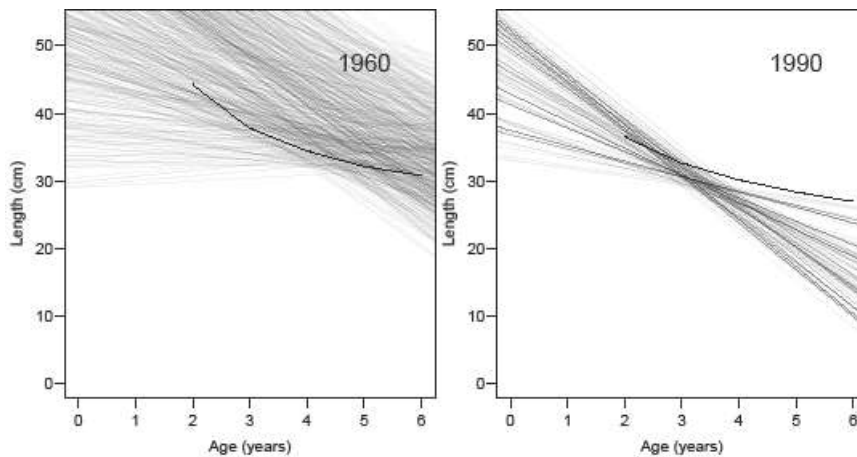
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652 Figure 7: North Sea plaice. 50% contours from simulation-based model fitting (grey)
653 superimposed on curves from previous work (black): (a) new model fit for 1960
654 against 1955-1964 cohorts from Grift et al (2002), (b) 1990 against 1985-1994.

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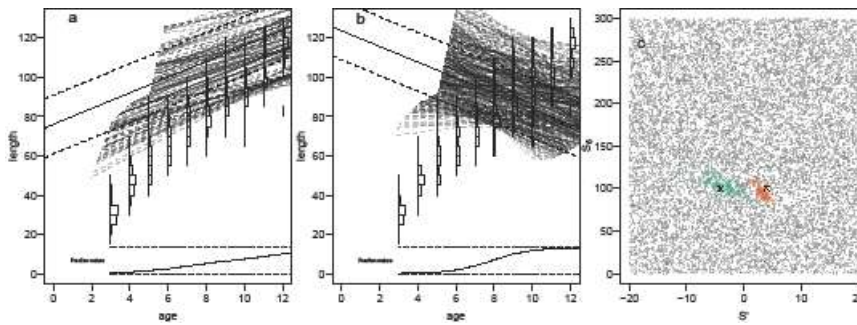
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663 Figure 8: Validation of selection of slope parameter. PMRN contours from new
664 algorithm overlaid on synthesised data (presentation as in Figure 3b) and actual
665 PMRN (black) for (a) actual positive slope of 4 cm yr^{-1} , (b) actual negative slope of -4
666 cm yr^{-1} . (c) bayesian 95% confidence interval of model parameters for (A) negative
667 slope and (B) positive slope, actual model parameters marked by crosses, dots are
668 tested parameters (as in Figure 4).

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