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Technical Note: Bayesian Fitting of Probabilistic Maturation Reaction Norms to Population-level Data

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Abstract

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

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

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

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

1. Introduction

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

A range of techniques for fitting PMRNs to different types of data are available, following a gradient from those requiring specialized data (Heino et al. 2002b) to those dealing with data collected routinely for other purposes (Barot et al. 2004a, Scott and Heikkonen 2012). Heino et al (2002b) constructed PMRNs for a cohort 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.

2. Theory and Calculation

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

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

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(observations | parameters)). Bayes' law then allows

137   these likelihoods to be converted into the posterior distribution of the parameters,

138   P(parameters | 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   P(mature | a, s_a) = P(mature | a-1, s_{a-1}) + P(immature | a-1, s_{a-1}) × $p(a, s)$ (3)

148   = P(mature | a-1, s_{a-1}) + (1 - P(mature | a-1, s_{a-1})) × $p(a, s)$

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

172

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

174    $\operatorname{logit}(p) = \log(p/(1-p))$ (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(parameters | 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(model | observations).

203

3. Methods and Materials

204

3.1 Northeast Arctic cod

205

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 $0 \le S_4 \le 60$, $-7 \le S' \le 7$

273 and $0 \le W \le 15$, based on the maximum length of plaice (52.1cm in the data set).

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 or 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

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 intersect

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.

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.

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.

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.

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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References

AFWG 2006. Report of the Arctic Fisheries Working Group. ICES CM 2006/ACFM:25, Copenhagen, Denmark.

Barot, S., Heino, M., O'Brien, L., Dieckmann, U. 2004a. Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. Evol. Ecol. Res. 6, 659-678.

Barot, S., Heino, M., O'Brien, L., Dieckmann, U. 2004b. Long-term trend in the maturation reaction norm of two cod stocks. Ecol. Appl. 14, 1257-1271.

Barot, S., Heino, M., Morgan, M.J., Dieckmann, U. 2005. Maturation of Newfoundland American plaice (*Hippoglossoides platessoides*): Long-term trends in maturation reaction norms despite low fishing mortality? ICES J. Mar. Sci. 62, 56-64.

Bogstad, B., Gjøsæter, H. 2001. Predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) in the Barents Sea: Implications for capelin stock assessment. Fish. Res. 53, 197-209.

Conover, D.O. 2000. Darwinian fishery science: 'Evolution' of fisheries science. Mar. Ecol. Prog. Ser. 208, 303-307.

Conover, D.O., Munch, S.B. 2002. Sustaining Fisheries Yields Over Evolutionary Time Scales. Science 297, 94-96.

Devine, J.A., Wright, P.J., Pardoe, H.E., Heino, M., Fraser, D.J., 2012. Comparing rates of contemporary evolution in life-history traits for exploited fish stocks. Canadian Journal of Fisheries and Aquatic Sciences 69, 1105–1120.

Dieckmann, U., Heino, M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. Mar. Ecol. Prog. Ser. 335, 253-269.

Endler, J.A. 1980. Natural Selection on Color Patterns in *Poecilia reticulata*. Evolution 34, 76-91.

Ernande, B., Dieckmann, U., Heino, M. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proc. Roy. Soc. B 271, 415-423.

Grift, R.E., Heino, M., Rijnsdorp, A.D., Kraak, S.B.M., Dieckmann, U. 2007. Three-dimensional maturation reaction norms for North Sea plaice. Mar. Ecol. Prog. Ser. 334, 213-224.

474 Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M., Dieckmann, U. 2003. Fisheries-
475   induced trends in reaction norms for maturation in North Sea plaice. Mar. Ecol.
476   Prog. Ser. 257, 247–257.

477 Heino, M. 1998. Management of evolving fish stocks. Can. J. Fish. Aquat. Sci. 55,
478   1971-1982.

479 Heino, M., Dieckmann, U., Godø, O.R. 2002a. Estimating reaction norms for age and
480   size at maturation with reconstructed immature size distributions: A new
481   technique illustrated by application to Northeast Arctic cod. ICES J. Mar. Sci. 59,
482   562-575.

483 Heino, M., Dieckmann, U., Godø, O.R. 2002b. Measuring probabilistic reaction
484   norms for age and size at maturation. Evolution 56, 669-678.

485 Heino, M., Dieckmann, U., Godø, O.R. 2002c. Reaction norm analysis of fisheries-
486   induced adaptive change and the case of the Northeast Arctic cod. ICES CM
487   Y:14, Copenhagen, Denmark.

488 Hendry, A.P., Kinnison, M.T. 1999. Perspective: The pace of modern life: Measuring
489   rates of contemporary microevolution. Evolution 53, 1637-1653.

490 Hjermann, D.O., Bogstad, B., Eikeset, A.M., Ottersen, G., Gjøsæter, H., Stenseth,
491   N.C. 2007. Food web dynamics affect Northeast Arctic cod recruitment. Proc.
492   Roy. Soc. B 274, 661-669.

493 Jørgensen, T. 1990. Long-term changes at age at sexual maturity of Northeast Arctic
494   cod. ICES J. Mar. Sci. 46, .

495 Jorgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K.,
496   Ernande, B., Gardmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K.,
497   Silva, A., Vainikka, A., Dieckmann, U., Heino, M., Rijnsdorp, A.D. 2007.
498   Ecology: Managing Evolving Fish Stocks. Science 318, 1247-1248.

499 Kenchington, E., Heino, M., Nielsen, E.E. 2003. Managing marine genetic diversity:
500   Time for action? ICES J. Mar. Sci. 60, 1172-1176.

501 Kraak, S.B.M. 2007. Does the probabilistic maturation reaction norm approach
502   disentangle phenotypic plasticity from genetic change? Mar. Ecol. Prog. Ser. 335,
503   295-300.

504 Kuparinen, A., Merilä, J. 2007. Detecting and managing fisheries-induced evolution.
505   Trends Ecol. Evol. doi:10.1016/j.tree.2007.08.011, .

506 Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES J. Mar. Sci. 57,
507   659-668.

508 Law, R., Grey, D.R. 1989. Evolution of yields from populations with age-specific
509   cropping. Evol. Ecol. 3, 343-359.

Lee, J.M., Appugliese, D., Kaciroti, N., Corwyn, R.F., Bradley, R.H., Lumeng, J.C. 2007. Weight status in young girls and the onset of puberty. Pediatrics 119, 624-630.

Loeng, H., Drinkwater, K., 2007. An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. Deep Sea Research Part II: Topical Studies in Oceanography 54, 2478–2500.

Marshall, C.T., McAdam, B.J. 2007. Integrated perspectives on genetic and environmental effects on maturation can reduce potential for errors of inference. Mar. Ecol. Prog. Ser. 335, 301-310.

Marshall, C.T., Needle, C.L., Thorsen, A., Kjesbu, O.S., Yaragina, N.A. 2006. Systematic bias in estimates of reproductive potential of an Atlantic cod (Gadus morhua) stock: implications for stock-recruit theory and management. Can. J. Fish. Aquat. Sci. 63, 980-994.

Marshall, C.T., Needle, C.L., Yaragina, N.A., Ajiad, A.M., Gusev, E. 2004. Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. Can. J. Fish. Aquat. Sci. 61, 1900-1917.

Morita, K., Fukuwaka, M. 2006. Does size matter most? The effect of growth history on probabilisitic reaction norm for salmon maturation. Evolution 60, 1516-1521.

Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., Peterson, C.H. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315, 1846-1850.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceeded the collapse of northern cod. Nature 428, 932-935.

Ottersen, G., Michalsen, K., Nakken, O. 1998. Ambient temperature and distribution of North-East Arctic cod. ICES J. Mar. Sci. 55, 67-85.

Pinnegar, J.K., Jennings, S., O'Brien, C.M., Polunin, N.V.C. 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. Ecology 39, 377-390.

Plaistow, S.J., Lapsley, C.T., Beckerman, A.P., Benton, T.G. 2004. Age and size at maturity: Sex, environmental variability and developmental thresholds. Proc. Roy. Soc. B 271, 919-924.

Reznick, D.N. 1990. Plasticity in age and size at maturity in male guppies(*Poecilia reticulata*): An experimental evaluation of alternative models of development. J. Evol. Biol. 3, 185-203.

Rowell, C.A., 1993. The effects of fishing on the timing of maturity in North Sea cod (*Gadus morhua* L.). In Stokes, T.K., McGlade, J.M., Law, R. (eds.) ,The Exploitation of Evolving Resources, Springer-Verlag, pp. 44–61.

549   Scott, R.D., Heikkonen, J., 2012. Estimating age at first maturity in fish from change-
550   points in growth rate. Mar Ecol Prog Ser 450, 147–157. doi:10.3354/meps09565

551   Stearns, S.C., Crandall, R.E., 1984. Plasticity for age and size at sexual maturity: A
552   life-history response to unavioidable stress. In Potts, G., Wootton, R.J. (eds.)
553   ,Fish Reproduction, Academic Press, pp. 13-33.

554   Stearns, S.C., Koella, J.C. 1986. The Evolution of Phenotypic Plasticity in Life-
555   History Traits: Predictions of Reaction Norms for Age and Size at Maturity.
556   Evolution 40, 893-913.

557   Stokes, K., Law, R. 2000. Fishing as an evolutionary force: 'Evolution' of fisheries
558   science. Mar. Ecol. Prog. Ser. 208, 307-309.

559   WGSSDS 2006. Report of the Working Group on the Assessment of Southern Shelf
560   Demersal Stocks. ICES CM 2006/ACFM:33, Copenhagen, Denmark.

561   Yndestad, H., 2003. The code of the long-term biomass cycles in the Barents Sea.
562   ICES J. Mar. Sci. 60, 1251–1264.

563   Table 1: Simulation-based algorithm for finding likelihood P(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_recruit <= a <= a_max}).

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569   1. For each age class, a, a_recruit <= a <= a_max

570   2.   Repeat R replicates for this age, recording numberthat are successful

571   3.   Expected number of mature fish comes from m_a in the ogive $F_{exp} =$

572   round($F\,m_a$)

573   4.   Draw F fish lengths, {s_i | 0 <= i < F} from the length distribution for

574   age a

575   5.   For each of these F simulated fish

576   6.   Calculate probability P(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(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 $F_{sim} = F_{exp}$ then this trial is successful at age a

583   10.   Likelihood at this age, P(observations a|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(observations | S_0, S', W)* = PROD(FOR ALL a)(P(observations a|S_0, S', W))
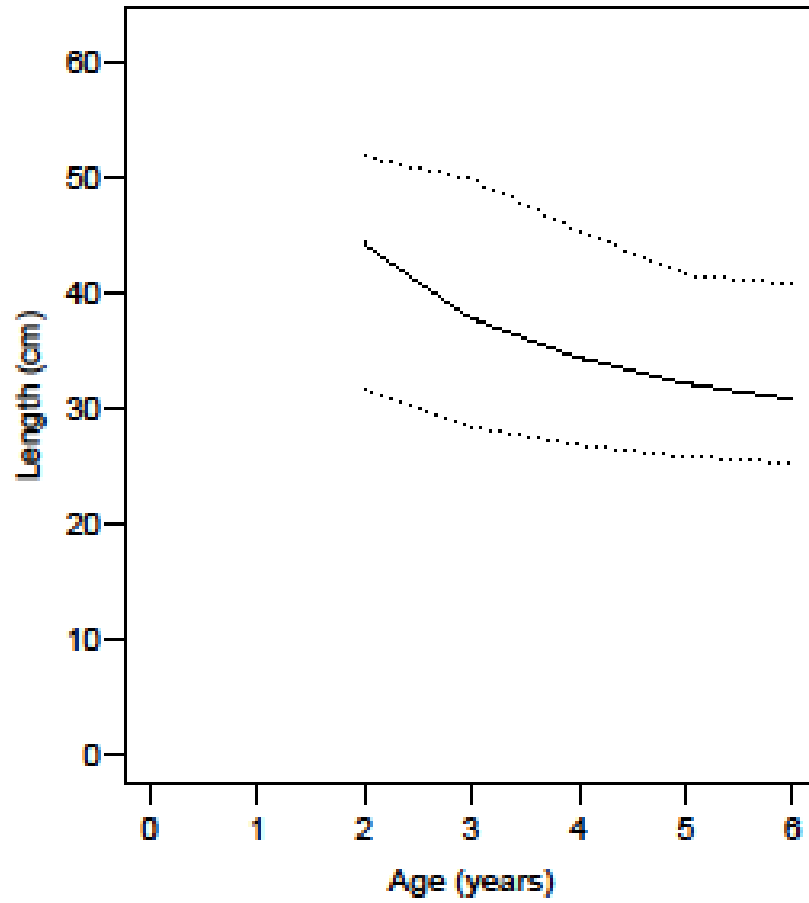
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591   Figure 1: PMRNs for North Sea plaice 1955-1964 cohorts (redrawn from values in

592   Grift et al (2003)). Solid line is 50% probability of maturation; dotted lines are 25%

593   and 75%.

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

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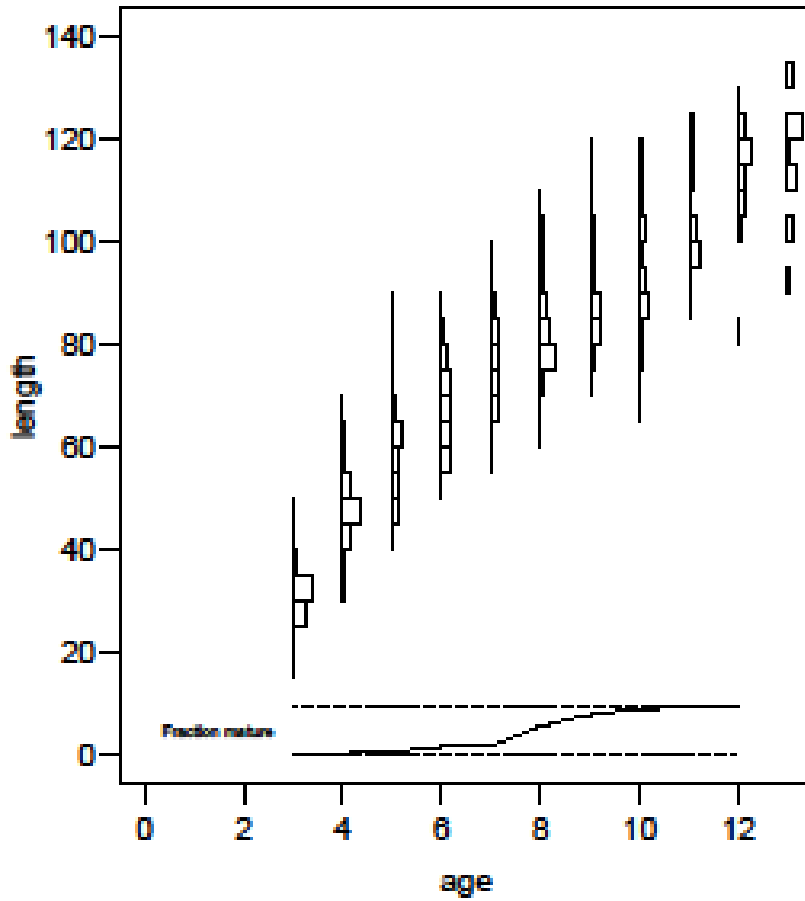
Figure 3: NEA cod. (a) Single best model, and (b) 95% bayesian confidence interval

for 1980 cohort (the models that accounted for 95% of all matches between a

simulation and observations, line denity indicative of posterior probability). Solid

lines are the 50% probability of maturation contour. Dotted lines are 25% and 75%

probability. Lines are cropped to cover only age-length combinations of NEA cod

that have been observed. Other features as Figure 2.

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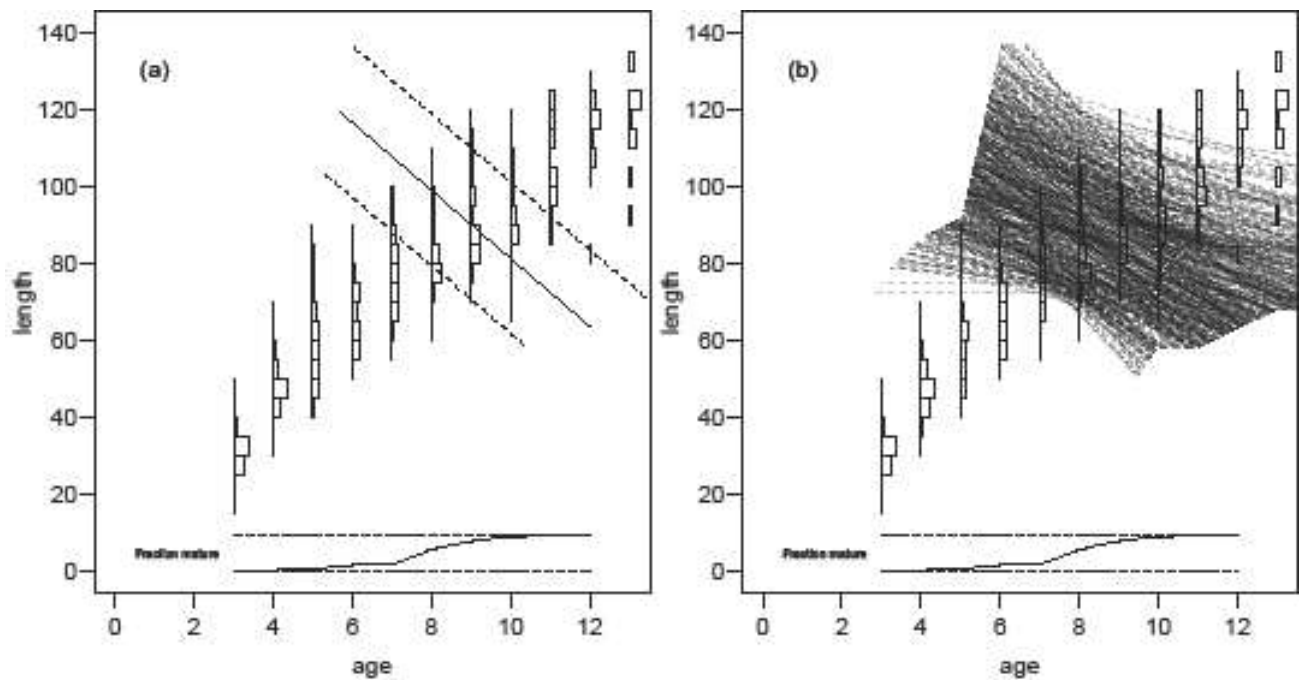
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618   Figure 4: Parameter space for PMRNs for NEA cod, and results for four evenly-

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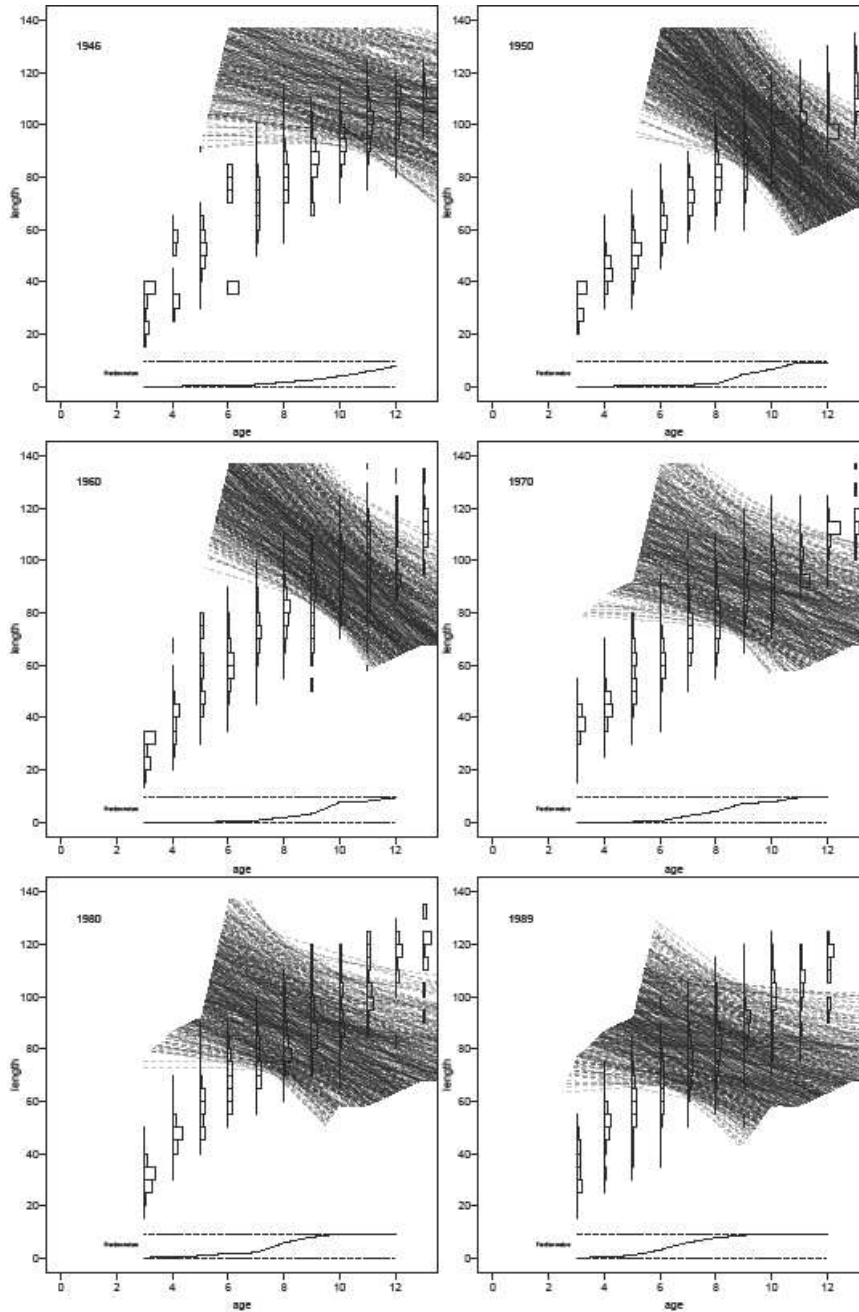
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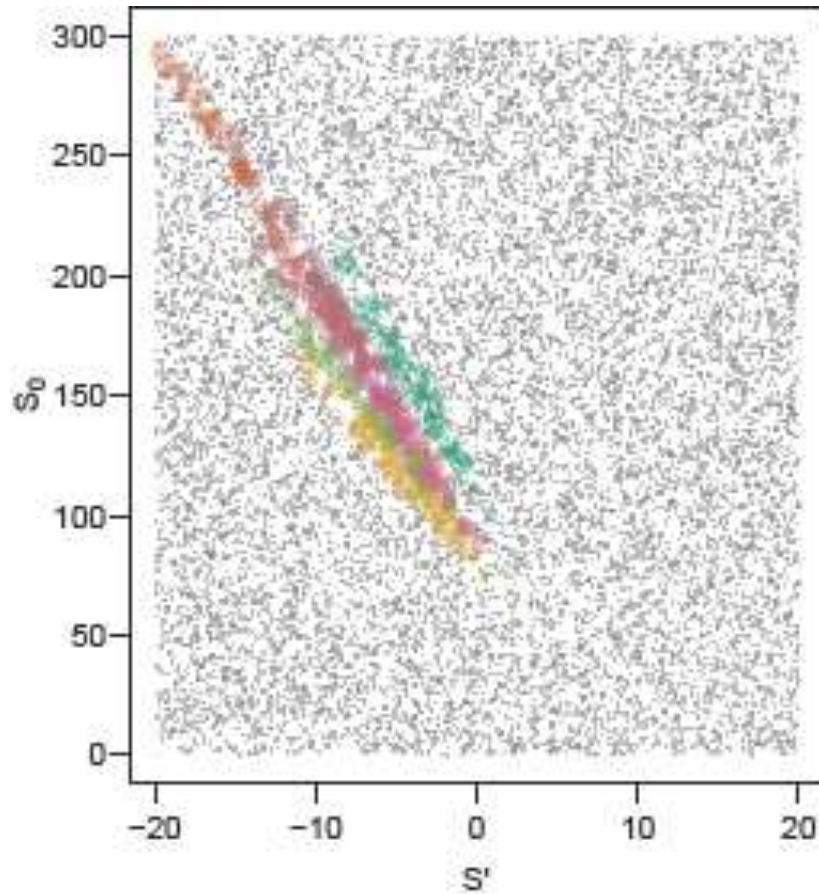
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635   Figure 5: Plots of the PMRNs from Figure 4 (a) 1946, (b) 1960, (c) 1974, (d) 1989.

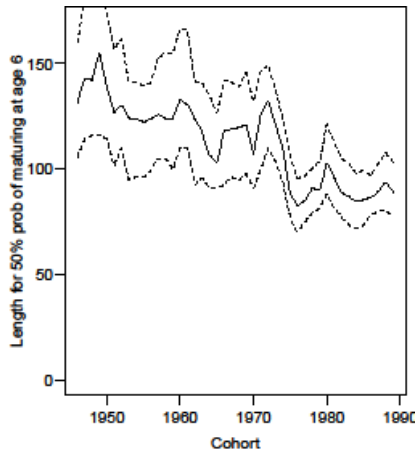636   Presentation as in Figure 3b.

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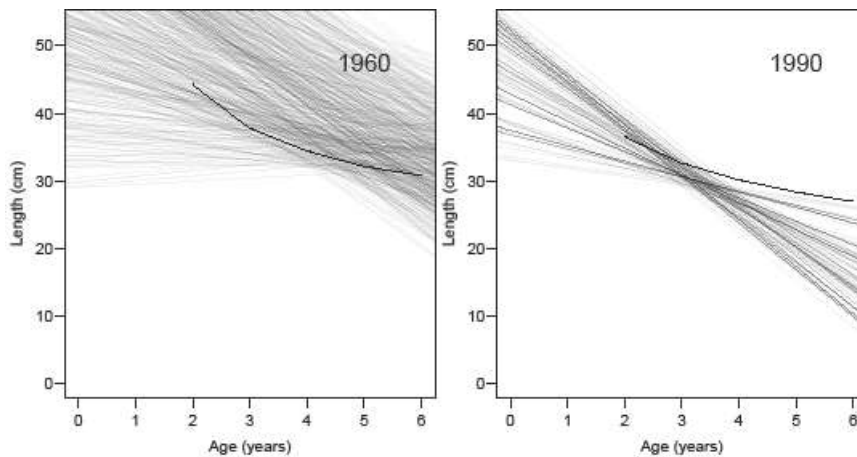

Figure 7: North Sea plaice. 50% contours from simulation-based model fitting (grey) superimposed on curves from previous work (black): (a) new model fit for 1960 against 1955-1964 cohorts from Grift et al (2002), (b) 1990 against 1985-1994.

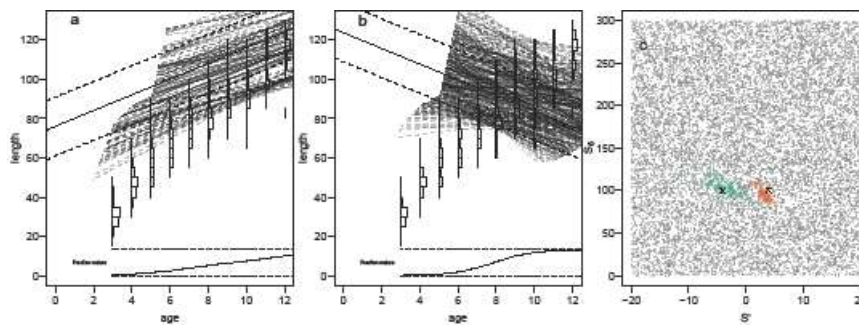Figure 8: Validation of selection of slope parameter. PMRN contours from new

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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