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1 Investigating the drivers of maturation dynamics in Barents Sea haddock (*Melanogrammus*
2 *aeglefinus*)

3

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11

12 **ABSTRACT**

13 Changes in size and age at maturation of many exploited fish stocks have been investigated
14 and the influences of environmental factors and exploitation have often been inferred, but not
15 explicitly investigated. Here we determine probabilistic maturation reaction norms (PMRNs)
16 for Barents Sea haddock (*Melanogrammus aeglefinus*) using generalized linear models
17 (GLM) and mixed effect models (GLMMs), which account for the correlation among samples
18 within a tow station, and investigate the effects of fishing mortality, environmental factors
19 (NAO, water temperature, and salinity), and potential density dependence or species
20 interaction effects. We found little evidence of a consistent trend in maturation tendencies for
21 Barents Sea haddock for cohorts 1983–2003, ages 4–6 years. Female haddock matured at
22 larger lengths for a given age than males, but overall patterns were similar for both sexes. The
23 GLMM approach gave consistently higher PMRN midpoint estimates than the GLM

24 approach, which indicated that PMRNs that do not account for correlations within the data
25 may bias estimates. Environmental factors, rather than exploitation, density dependence, or
26 species interactions, were responsible for the observed changes in size and age at maturation
27 in Barents Sea haddock during the late 1980s through early 2000s. Little evidence of
28 fisheries-induced evolution was found in these fish over the time period investigated. The lack
29 of a significant temporal trend in maturation may be due to several challenges in estimating
30 representative population parameters for this stock, the trait change being in a period of stasis
31 or reversal, or adaptation by the fish to higher exploitation in the past resulting in negligible
32 evolutionary selection during the study period when exploitation has been more moderate.

33

34 Keywords: Barents Sea, haddock, life history, maturation, *Melanogrammus aeglefinus*,
35 probabilistic maturation reaction norms

36

37 **1. Introduction**

38 Harvesting of wild populations is not random selection. Humans are capable of generating
39 relatively rapid phenotypic changes within harvested populations by targeting individuals of
40 certain sizes, age classes, or behaviours (Hendry et al., 2008; Darimont et al., 2009).

41 Concentrated and high selection pressure on individuals can result in genetic changes in the
42 population if the selected phenotype has a partial genetic basis (Miller, 1957; Ricker, 1981;
43 Nelson and Soulé, 1987; Rijnsdorp, 1993a; Law, 2000). Life history traits that have a partial
44 genetic basis and have been shown to evolve under selective pressures include age and size at
45 maturation (Silliman, 1975; Reznick et al., 1990; Reznick and Ghalambor, 2005),
46 reproductive effort (Rijnsdorp et al., 2005), growth (Conover and Munch, 2002; Conover et

47 al., 2005; Neuheimer and Taggart, 2010), and fecundity (Thomas et al., 2009). Traits also
48 evolve in response to changing environmental conditions, which include density dependent
49 growth responses resulting from changes in intraspecific or interspecific competition,
50 oceanographic conditions, and changes in prey availability or type (Stokes et al., 1993).
51 Pinpointing whether trait change is a result of phenotypic plasticity or genetic evolution must
52 either depend on molecular genetic analysis or common-garden experiments, which are
53 relatively rare, or weaker approaches, such as regression or reaction norm methods
54 (Dieckmann and Heino, 2007).

55 Probabilistic maturation reaction norms (PMRNs) have been suggested as a method to
56 disentangle the effects of phenotypic plasticity from genetic effects on maturation (Heino et
57 al., 2002b). By describing the probability of becoming mature as a function of age and size,
58 PMRNs are thought to remove the main effects of varying mortality and juvenile growth rates
59 (Dieckmann and Heino, 2007). However, the PMRN approach has limitations. Reaction
60 norms for age and length at maturation do not account for factors other than growth-related
61 phenotypic plasticity in maturation (Dieckmann and Heino, 2007; Uusi-Heikkilä et al., 2011),
62 nor do they disentangle all effects of growth variability on maturation, neither in theory
63 (Heino and Dieckmann, 2008) nor in practice (Morita and Fukuwaka, 2006; Morita et al.,
64 2009). When possible, other variables should be included in the maturation reaction norm
65 estimation, and some work has investigated higher-dimensional reaction norms, which
66 included the effects of condition and temperature on the maturation process (Baulier et al.,
67 2006; Grift et al., 2007; Mollet et al., 2007; Vainikka et al., 2009a). Yet imperfect
68 disentanglement does not make the PMRN approach invalid. PMRNs remove the plastic
69 effects of varying average juvenile somatic growth rates from the description of the
70 maturation schedule (Dieckmann and Heino, 2007), and this is already an improvement over
71 indices that are sensitive to growth variability, such as maturity ogives. Often unaccounted

72 effects, such as condition and water temperature, can be seen as contributing “mere” noise to
73 estimation. However, when unaccounted effects show trends, they may introduce spurious
74 trends to PMRNs or mask true trends (Dieckmann and Heino, 2007; Heino and Dieckmann,
75 2008). As with any other statistical tool, results from PMRN analyses must be interpreted
76 critically.

77 PMRNs have been used to investigate changes in size and age at maturation for many
78 commercial fish stocks (e.g., Heino and Dieckmann, 2008; Wang et al., 2008; Pardoe et al.,
79 2009; Vainikka et al., 2009a; Vainikka et al., 2009b; van Walraven et al., 2010; Swain, 2011),
80 and the general concession has been that an important factor for the observed changes is
81 exploitation. Furthermore, fishing pressure explained the observed changes in life history
82 traits for the majority of the 37 fish stocks investigated by (Sharpe and Hendry, 2009). Most
83 PMRN studies assessing changes in size and age at maturation have not explicitly evaluated
84 the contribution of environmental factors, although there are a few exceptions (e.g., Heino et
85 al., 2002c; Mollet et al., 2007; Pardoe et al., 2009; van Walraven et al., 2010).

86 Changes in PMRNs have been or currently are being investigated for two of the main
87 commercial species in the Barents Sea, Northeast Arctic cod (*Gadus morhua*; Heino et al.,
88 2002c) and capelin (*Mallotus villosus*; L. Baulier, in prep.). Haddock (*Melanogrammus*
89 *aeglefinus*) is the second most important commercial groundfish species in the Barents Sea.
90 Stock dynamics are characterized by large cyclic fluctuations (Olsen et al., 2010) and strong
91 recruitment pulses, thought to be partially linked to water temperatures (ICES, 2008). The
92 exploitation rate of haddock has been variable, with a peak catch of 322,000 t occurring in
93 1973; catches in the last decade have been in the range of 150,000 – 200,000 t (ICES, 2010).
94 Haddock is currently classified as “harvested sustainably”, although unreported discarding is
95 thought to be an issue (ICES, 2010). The main spawning grounds are located to the west and

96 south of the Barents Sea, along the Norwegian shelf edge (Solemdal et al., 1989), and mature
97 fish typically migrate from the central and eastern areas of the Barents Sea. Spawning is
98 between March and June, with most fish spawning at the end of April (ICES, 2010). Age at
99 50% maturity in haddock has fluctuated since 1980, but does not show a consistent trend
100 (ICES, 2010).

101 Here we investigate whether Barents Sea haddock show evidence of changing age and size at
102 maturation between 1981–2009. The stock has been exploited at a higher rate for several
103 decades prior to investigation (ICES, 2010). We use PMRNs to analyze temporal trends in
104 maturation tendency, where the reaction norm method describes the probability that an
105 immature fish will mature during a given time interval and at a certain size and age (Heino et
106 al., 2002b). Since the approach accounts for most of the effects of phenotypic plasticity in
107 growth, we investigate secondary factors, usually not included in PMRN analyses, that might
108 explain any observed trends; these included the effects of fishing mortality, environmental
109 factors from three areas of the Barents Sea (water temperature and salinity), the North
110 Atlantic Oscillation (NAO) index, and potential density dependence or species interaction
111 effects. We use both generalized linear models and generalized linear mixed models.
112 Generalized linear models are the method typically employed in PMRN analyses because of
113 their ease of use; however, generalized linear mixed models naturally allow accounting for
114 correlations within the data, which can lead to incorrect statistical conclusions if ignored
115 (Smith et al., 2009). We used mixed models to incorporate the knowledge that size, age, and
116 maturation status of fish sampled from the same station in a given year are likely highly
117 correlated and to investigate if ignoring such correlation led to large differences in maturation
118 estimates and trends.

119 **2. Methods**

120 Data were collected by the Institute of Marine Research (Bergen, Norway) during the winter
121 Barents Sea research surveys (late January–early March), in 1981–2009. Immature and
122 mature fish were identified based on the maturation status of their gonads. All fish of
123 maturation stage 1, without evidence of spawning zones on otoliths, were considered
124 immature. Newly matured fish (recruit spawner) and repeat spawners were differentiated on
125 the basis of otolith patterns, or the number of spawning zones apparent on the otolith; this is
126 similar to the procedure used for determining cod (Rollefsen, 1933) and halibut
127 (*Hippoglossus hippoglossus*; Devold, 1938) recruit spawners. Fish were retained in the
128 analysis if the otolith readability scores were 1 (zones counted and measured with certainty)
129 or 2 (zones may be counted, but not measured).

130 Analyses were restricted to ages where first-time spawning fish appeared in the data. Data
131 were restricted to cohorts 1983–2003 and ages 4–6 for both sexes on account of too few data
132 for recruit spawners from other cohorts and ages. Approximately 3,000 recruit spawner and
133 10,300 immature fish measurements were used in the analyses (Table A.1).

134 The survey is thought to disproportionately target the immature fraction of the stock as mature
135 fish are beginning to migrate to spawning areas at this time (Aglen et al., 2005). Therefore the
136 proportions of immature and maturing fish in the survey data may not reflect the true
137 proportions in the population. In this scenario, the length at maturation estimate will be biased
138 high because the distribution is skewed towards immature fish. To account for potential biases
139 in sampling, immature fish were down-weighted by the ratio of the proportion of maturing
140 fish estimated from the ICES maturity ogive for the joint Russian-Norwegian winter survey
141 combined with the Russian autumn survey (ICES, 2009) to that estimated only from the
142 winter survey data. The ogives estimated from the combined autumn and winter survey data

143 are believed to better represent the proportions of immature and mature fish. The proportion
144 of maturing fish $m(a)$ was estimated from the maturity ogive $o(a)$ at age a and $a-1$ as:

$$145 \quad m(a) = \frac{o(a) - o(a-1)}{1 - o(a-1)} \quad (1)$$

146 (Barot et al., 2004). If data from the Barents Sea winter survey were representative of the
147 stock, then the ratio would equal one and no weighting would occur.

148 The amount of area surveyed was standardized from 1981–1993, after which it was expanded
149 and the amount of coverage depended on ice extent, Norwegian access to the Russian EEZ (or
150 vice versa), or Russian involvement in the survey (coverage of Russian waters by Russian
151 vessels; details in Aglen et al., 2005). To account for the changing survey area, the ratio of
152 area covered in a particular year to the maximum area surveyed (all years; ICES, 2009) was
153 used to weight the proportions of maturing fish. Maximum area was from the 1995 survey.

154 The effects of weighting the data were tested in a sensitivity analysis by 1) ignoring the
155 potential unrepresentative sampling of juvenile relative to mature fish, 2) ignoring the change
156 in areal extent of the survey, and 3) removing both forms of weighting. Weighting terms that
157 accounted for these factors were removed sequentially from the final model and the effects on
158 model fits, residual deviance, the random intercept term, and PMRN midpoints were
159 investigated. The sensitivity analysis was only performed on the generalized linear mixed
160 model.

161 *2.1 Probabilistic maturation reaction norm method*

162 The direct method of estimating PMRNs developed by (Heino et al., 2002b) was adapted for
163 use with generalized linear mixed models (GLMMs). A GLMM with a binomial error
164 distribution and logit link function, a random intercept term, data weights as defined above,

165 and the Laplace approximation of likelihood were used (Bates and Maechler, 2010). The
166 Laplace approximation allows the use of likelihood-based inference (Bolker et al., 2009),
167 which was necessary for determining model choice. Likelihood ratio tests are adequate for
168 testing fixed effects (model selection) in GLMMs when the ratio of the total sample size to
169 the number of fixed-effect levels being tested is large (Pinheiro and Bates, 2000) and the
170 number of random-effect levels are large (Demidenko, 2004; Bolker et al., 2009). The full
171 mixed model with all possible interactions and a random intercept was the base model. The
172 random intercept term was a unique station + year identifier; stations are pre-defined for the
173 bottom trawl survey in the Barents Sea (see Aglen et al., 2008) for details and station
174 placement). Haddock distribution appears to be based on size and/or age and distributions are
175 relatively consistent over time (Aglen et al., 2000; Aglen et al., 2005; Aglen et al., 2008). The
176 random intercept term implies that the probability of a fish becoming mature at a given station
177 in a given year is correlated with other fish of the same size and age at that station and time,
178 and indicates that increasing the number of samples within a station provides less new
179 information than sample size would normally signify. This correlation has been shown to be
180 positive for maturity ogives (Korsbrekke, 1999) and other parameters (Pennington and
181 Vølstad, 1994). Model fits, standard errors of parameter estimates, and residual plots were
182 also used to assess models.

183 PMRNs were also estimated with generalized linear models (GLM) for comparison with
184 GLMM models. GLMs treat each fish as an independent sample and any correlations between
185 samples within a station are ignored; this is how data are typically treated when estimating
186 probabilistic maturation reaction norms. Data were under-dispersed for GLM models, thus a
187 quasibinomial error distribution with logit link function was used. The quasi-AIC (QAIC) was
188 estimated as $Deviance/Dispersion + (2 * (df + 1))$ where df is the number of degrees of
189 freedom (Burnham and Anderson, 2002).

190 For all models, length was included as a continuous variable, while age and cohort were first
191 fit as factors and then as continuous variables. Once a model using only length, age, cohort,
192 and interaction terms was chosen, other explanatory factors were added. Likelihood ratio tests
193 were again used to compare models with additional explanatory terms. Models were also
194 assessed using standard errors of parameter estimates and residual plots.

195 *2.2 Randomization tests and confidence intervals*

196 Randomizations were used to investigate if the observed differences for sex, cohort, and age
197 in the maturation reaction norms were real (Barot et al., 2004). For example, the hypothesis
198 that males and females had different PMRNs was tested by creating a new data set, where sex
199 values were randomly assigned to individuals within each cohort and age. Within the new,
200 randomized datasets, the probability of maturing was modelled using GLMs, with a
201 quasibinomial error structure and logit link, and included length as a continuous variable and
202 data weights (as defined above). The randomization procedure was repeated 1000 times and
203 the likelihood ratio F statistic, testing the sex effect, was collected. The effect was considered
204 significant if less than 5% of the randomizations led to a higher value of the test statistic than
205 that computed from the original data. A similar procedure was also used to test whether
206 cohorts or ages had different reaction norms. GLMs, and not GLMMs, were used because
207 while both models gave similar results, GLMs took much less time to run (minutes per model
208 as opposed to days).

209 Confidence intervals for the length at 50% probability of maturing (L_{p50}) were also estimated
210 with bootstrapping and randomization approaches. Tows were randomly resampled within a
211 year to recreate a new data set from which reaction norm estimates were derived. This process
212 was repeated to obtain 1000 estimates of the reaction norm, and the distribution of the
213 endpoints was then used to derive the 95% confidence intervals (Manly, 1991).

214 *2.3 Explanatory factors*

215 Environmental data were extracted from databases at the Institute of Marine Research and
216 were chosen to represent habitat of haddock lifestages and their food (Olsen et al., 2010).
217 Oceanographic data from the Fugløy-Bear Island transect (70°30' N, 20°30' E – 74°15' N,
218 19°10' E, 0–200 m) provided an estimate of temperature and salinity from the influx of
219 Atlantic water and are considered representative of the western Barents Sea (Stiansen et al.,
220 2005). Water temperature from the Vardø-North section (31°13' E, 76°30' N – Vardø) was
221 used to represent the central part of the Barents Sea (Ingvaldsen et al., 2006), while data from
222 the Kola transect (33°00' E, 77°30' N – 72°30' N, 0–200 m) provided an indicator of thermal
223 and salinity conditions for the southern and eastern Barents Sea (Bochkov, 1982). The North
224 Atlantic Oscillation (NAO) winter index was used as a measure of the strength of large-scale
225 atmospheric circulation (www.cgd.ucar.edu/cas/jhurrell/indices.html). Positive anomalies
226 appear to be related to northward shifts of the Gulf Stream, more frequent and intense storms
227 in the vicinity of the Norwegian Sea (Hurrell and Deser, 2009), and greater inflow of warmer
228 water into the Barents Sea (Hurrell and Dickson, 2004). The total estimated biomass of cod,
229 haddock, capelin and ratio of capelin to cod biomass were used to represent potential species
230 interactions. Capelin and cod were included because capelin is the primary fish prey of
231 haddock, while cod are known to include a proportion of small haddock in their diet,
232 especially in years of low capelin biomass (Stiansen et al., 2005; Olsen et al., 2010). The ratio
233 of capelin to cod biomass was used as an indicator of higher predation upon haddock. The
234 direct effect of fishing on reaction norms was tested by including fishing mortality (F , year⁻¹),
235 which was a proxy for the strength of selection imposed by the fishery. Haddock are regulated
236 by a TAC, minimum bottom trawl mesh size of 135 mm (125 mm in the Russian EEZ),
237 sorting grids since 1997, and a minimum size limit of 44 cm (39 cm in the Russian EEZ;
238 ICES, 2010). Trawls with a mesh range of 135–140 mm have a 50% retention of haddock of

239 47–53 cm average length and have a selection range, i.e., the length range over which
240 retention increases from 25% to 75%, of 38–66 cm (Halliday et al., 1999; Huse et al., 2000).
241 Because regulations have remained fairly static over the time period of the study, we assumed
242 that size selection should have been similar from year to year.

243 The “decision” to mature occurs long before the process of spawning begins (Wright, 2007).
244 The maturation process has been suggested to take up to three years for North Sea plaice
245 (Rijnsdorp, 1993b; Grift et al., 2003) and one year for North Sea haddock (Tobin et al., 2010).
246 Because the length of time between “deciding” to mature and spawning is unknown for
247 Barents Sea haddock, the effect of explanatory variables one and two years before first
248 spawning was tested. For fishing mortality, the effect seven years before first spawning was
249 also included (lag = 7); this is the generation time for Barents Sea haddock, approximated
250 using the method of (Froese and Binohlan, 2000) and data from ICES (2010). All explanatory
251 factors were standardized to a mean of zero and a standard deviation of one, thereby creating
252 unit-less indices, rescaled around zero (Fig. 1). Correlations between explanatory factors were
253 tested to ensure highly correlated factors were not included in the same model.

254 **3. Results**

255 *3.1 Length-at-age*

256 Average size of immature and recruit-spawning haddock increased with age (Fig. 2). Recruit
257 spawners were, on average, 4 cm larger than immature fish of the same age. Age 4 fish
258 showed the largest size differences between immature and mature fish. All ages generally
259 indicated a stable average size, but showed a sharp increase for cohorts in the mid- to late
260 1980s, and a decrease in size in the early to mid 1990s. For cohorts from the 1980s, difference
261 in size between immature and recruit spawning fish was less (e.g., age 4, both sexes) or

262 immature fish were larger than recruit spawners (e.g., age 6 males), which indicated sampling
263 may not have been representative of the population.

264 3.2 Maturation reaction norm

265 The sample sizes of recruit spawners were too low to use the full model, which included *age*,
266 *year*, *cohort*, and all the interaction terms (i.e., $age \times cohort + length \times age + length \times cohort$
267 $+ length \times age \times cohort$). GLM and GLMM models that best described the probability of
268 maturing for haddock were the same for fish of each sex:

269 Males: $\text{logit}(\text{maturation}) \cong c_0 + c_1 \text{length} + c_2 \text{age} + c_3 \text{cohort} + c_4 (\text{age} \times \text{cohort})$, and

270 Females: $\text{logit}(\text{maturation}) \cong c_0 + c_1 \text{length} + c_2 \text{age} + c_3 \text{cohort} + c_4 (\text{length} \times \text{age})$,

271 where length and age were fit as continuous variables, and cohort was included as a factor
272 (i.e., a classifying variable). Including the $age \times cohort$ interaction was needed to detect age-
273 dependent temporal changes in the probability of being mature, while the $length \times age$
274 interaction in the female model allowed the width of the reaction norm to become age-
275 dependent and detected length-dependent changes in the probability of maturing. Although
276 randomization tests showed that no significant differences between ages existed, adding age
277 to the models improved the fit of the model and was necessary to allow for commonly
278 observed differences between age-classes.

279 The environmental terms that best described trends in the probability of maturing differed
280 between sexes. The Vardø-North section temperature index two years before the maturation
281 event explained the variation in males (GLMM and GLM results), while water temperature
282 from the Fugløya-Bear Island section one year and salinity from the Kola section two years
283 before the maturation event explained the variation in trends in females (GLMM results;
284 Table 1). Water temperature had a positive effect on maturation whereas salinity had a

285 negative one (Table 1). The Kola section salinity-only model appeared to be the better GLM
286 model for females (Table 1) and the plotted L_{p50} estimates did not differ greatly from the two-
287 environmental term model (except for a few cohorts in age 5 and age 6; Fig. 3), indicating
288 that a more complex model may not be necessary. Exploitation, species interactions, and
289 density dependence did not explain the variation in estimates for either sex. The trend in L_{p50}
290 estimates for both GLMM and GLM models were relatively similar, but GLM estimates were
291 generally 1–3 cm smaller than GLMM estimates. In other words, not accounting for the
292 similarity of fish within the same trawl haul meant that L_{p50} was underestimated by as much
293 as 8% for males and 4% for females.

294 Females matured at a larger size for a given age than males. Females were, on average, 7.8 cm
295 larger than males when they attained 50% probability of maturing at age 4, 10.3 cm larger at
296 age 5, and 14.5 cm larger at age 6 when comparing midpoints from the GLMM approach. The
297 size difference between the sexes at maturation was slightly greater when comparing the
298 midpoints from the GLM approach: 10 cm for age 4, 11.9 cm for age 5, and 16.4 cm for age
299 6.

300 Estimates of reaction norm midpoints for males and females show a similar pattern; L_{p50}
301 estimates were smaller for cohorts before 1985 (Fig. 3). After 1985, PMRN midpoints
302 appeared to oscillate slightly, with lower values in the mid-1990s. A large amount of
303 uncertainty was apparent. The 1987 and 1994 male cohorts were poorly estimated as a result
304 of the low number of recruit spawners sampled (Table A.1). For both sexes at age 6, the
305 models fit poorly for those cohorts where the size of immature fish was equal to or greater
306 than the size of maturing fish. This could indicate that the sampling was not representative of
307 the population's true size structure. Result from t-tests indicated that the slightly increasing

308 trend in L_{p50} estimates for both sexes and all ages was not significantly different from zero (p
309 ≥ 0.12 for all cases; Table A.2).

310 *3.3 Sensitivity tests*

311 Removing the down-weighting of immature fish (to account for potential oversampling of
312 immature fish) and the weighting by survey area (to account for changes in the survey)
313 resulted in poorer model fits, less residual deviance explained, and higher variances
314 associated with the random intercept term (Table 1). Models without weights were
315 exceptionally poor fits for both males and females and removal of weighting affected which
316 explanatory terms improved the fit of the model. For example, removing all weighting from
317 the female model resulted in no explanatory terms significantly improving the model.
318 Accounting for differences in the amount of area surveyed each year appeared to be more
319 important than compensating for the undersampling of maturing fish. However, both
320 weighting terms were needed in the model, as seen in the higher remaining residual deviance
321 and random intercept term variance (Table 1). A higher variance in the random intercept term
322 indicated that the logistic curve estimated for each station had a vastly different intercept than
323 the final weighted model.

324 Maturation reaction norm midpoints were lower after accounting for potential sampling
325 issues. Ignoring that immature fish were most likely overrepresented in the trawl hauls
326 resulted in midpoints 3–5 cm larger, which was 5–12% larger than midpoints from the model
327 including all forms of weighting. Removing the weighting by survey area increased PMRN
328 midpoints by 1–4 cm (2–8%), while using no model weights resulted in maturation midpoints
329 8–21% larger for fish of a given age.

330 **4. Discussion**

331 We demonstrate that maturation tendencies of Barents Sea haddock vary sexually (i.e.,
332 females tend to mature at larger sizes for a given age than males), but show no specific trend
333 over the past three decades. Maturation tendency is variable and appears to reflect, at a
334 temporal lag, patterns in length at age. Increased length at first spawning has been reported in
335 haddock following reduced growth and therefore smaller size at age, usually as a result of
336 high abundance related to periodic strong recruitment pulses (Templeman et al., 1978;
337 Kovtsova, 1993; Korsbrekke, 1999; Korsbrekke, 2003). This may be an indication that, while
338 capturing most of the plastic effects of juvenile growth rate variations from the description of
339 the maturation schedule (Dieckmann and Heino, 2007), not all effects of growth variability on
340 maturation were removed by the PMRNs.

341 The probabilistic maturation reaction norm approach has suggested evolution in maturation
342 for numerous fish stocks (reviewed in Jørgensen et al., 2007; Heino and Dieckmann, 2008;
343 Sharpe and Hendry, 2009). The majority of these studies have used only age and size to
344 describe the maturation tendency. Here, we have included information on fishing mortality,
345 environmental factors, and inter- and intraspecies interactions within the PMRN model to
346 determine whether this information strengthens the explanatory power of these models.
347 Important factors for determining maturation in haddock (beyond body length) were western
348 Barents Sea temperature lagged one year (females), central Barents Sea temperature lagged
349 two years (males) and south/eastern Barents Sea salinity lagged two years (females). Water
350 temperature for the two regions was significantly correlated ($r = 0.54$, $p < 0.001$) and trends
351 were similar (Fig. 1a), which may explain why different factors were important for males and
352 females. When we tested the effect of swapping temperature factors for males and females,
353 western Barents Sea water temperature lagged one year was highly significant for males ($p <$
354 0.001) and central Barents sea temperature lagged two years was significantly related to
355 trends in females ($p = 0.01$), but model fits were better in the final chosen models for each

356 sex. Temperature has been increasing in the Barents Sea, with some variability, throughout
357 the period of interest; trends in salinity are similar to trends in temperature. Increased water
358 temperature can be due to overall higher water temperatures or because there is an increased
359 inflow of Atlantic water (Loeng et al., 1997), whereas increased salinity may be the result of
360 greater ice formation and subsequent brine release (Schauer et al., 2002) or increased inflow
361 of Atlantic water (Stiansen et al., 2005). Atlantic water volume flux has nearly doubled in the
362 past decade and warmer, more saline water has spread further eastward in the Barents Sea
363 (ICES, 2008). Increased inflow often results in increased nutrients and subsequent increased
364 abundance of planktonic organisms (Ottersen and Stenseth, 2001; Stiansen et al., 2005).
365 Changes in Atlantic inflow may also be reflected in current velocities and effect the transport
366 of larvae and zooplankton (Loeng et al., 1997). Gjøsæter and Loeng (1987) postulated that
367 current velocities and resultant transport played a role in large variations in growth of capelin
368 when water temperatures within the region did not vary annually.

369 Neither density dependent nor species interaction effects considered here accounted for
370 significant variability in the PMRN estimates. Environmental conditions have been shown to
371 override density dependent effects for species near the northern limit of their range (Ottersen
372 and Loeng, 2000). This is in contrast to what Heino et al. (2002c) found for Northeast Arctic
373 cod, where maturation in cod was influenced by feeding conditions (the amount of available
374 prey and high intraspecific competition for that prey), and the findings of Korsbrekke (1999),
375 who suggested that maturation in haddock was influenced by density dependence. The effect
376 of fishing mortality on haddock maturation probabilities was explicitly tested within the
377 reaction norms and was found not to contribute. Using fishing mortality as a proxy for
378 selection pressure is not as robust as using a metric that describes the size-selectivity of the
379 fishery. In years of high harvest rates, harvest rates for younger age classes were higher,
380 indicating age selectivity may exist in the fishery. The relationship between haddock

381 maturation and selection pressure warrants further investigation and is the next logical step,
382 especially since exploitation was higher in the three decades prior to this study. However, we
383 must reiterate that there is no temporal trend within the maturation reaction norm midpoints in
384 the past twenty years, indicating that there is little evolution occurring.

385 The motivation for using generalized linear mixed models, instead of the simpler generalized
386 linear models, is that the former allow a natural way to account for within-sample correlations
387 (Smith et al., 2009). Intra-sample correlations lead to effective sample sizes being lower than
388 the nominal ones, and ignoring this can lead to incorrect statistical inference. In our study,
389 however, the results from both approaches did not differ in any essential way: the temporal
390 patterns were similar and the underlying trend was not significantly different from zero. The
391 GLMM approach, however, did give consistently higher PMRN midpoint estimates than the
392 GLM approach. Thus, PMRNs that do not account for correlations within the data or nested
393 design may bias maturation reaction norm midpoints.

394 Sampling of haddock in the Barents Sea may not be representative of the population. Large
395 concentrations of mature haddock have been observed to often display pelagic behaviour
396 during the winter survey (Aglen et al., 2005), which would result in more immature fish being
397 captured. Mature fish also are often found high in the water column at night (Olsen et al.,
398 2010), which is long in the Barents Sea at the time of the survey. Since the survey operates
399 over 24-hours, it is possible that there are some catchability issues between day and night
400 sampling. Immature fish may be overrepresented in the catches also because mature haddock
401 begin migrating to the spawning grounds at the time of the survey, although it has been noted
402 that these are mainly the older, mature fish (age 7+; ICES, 2010) and not the ages used in this
403 analysis. Sampling of maturing individuals for a given age class was relatively consistent,
404 albeit low, in the analysis. The reaction norm method is considered insensitive to variability in

405 sampling intensity or gear size selectivity as long as the maturity proportions remain
406 unchanged (Heino et al., 2002a; Wang et al., 2008). Given the behavioural changes of
407 haddock with maturation and the movement of fish to the spawning ground around the time of
408 sampling, it is possible that the maturity proportions were affected. We attempted to correct
409 for this by applying a weighting factor to the numbers of immature fish based on the predicted
410 probability of maturing estimated from maturity ogives.

411 The changes in length at age of haddock in response to environmental conditions in this study
412 are similar to that of Korsbrekke (1999, 2003), who restricted his analysis to the central
413 region of the Barents Sea, an area consistently covered by the Norwegian Barents Sea
414 groundfish survey in all years. We choose to use all available data and weight by the
415 proportion of maximum survey area covered to downweight years of less coverage. Growth
416 changes presented here were also similar to trends in growth data from the Lofoten survey
417 (Korsbrekke, 2003), which surveys mainly the mature portion of the stock. This provides
418 some evidence that the winter survey sampling may not be inconsistent with stock dynamics.

419 Most studies investigating long-term trends in maturation reaction norms have revealed
420 changes that are suggestive of fisheries-induced evolution (summarized in Heino and
421 Dieckmann, 2008). Furthermore, other haddock stocks have shown changes suggestive of
422 fisheries-induced evolution (Neuheimer and Taggart, 2010). That Barents Sea haddock is an
423 exception to this pattern was unexpected. The lack of a clear trend might be because
424 consistent maturation changes did not take place during the study period, the trait change is in
425 a period of stasis or reversal, or that changes occurred, but we were unable to detect them. We
426 did not have any a priori reasons to expect no maturation evolution in haddock. A possible
427 explanation is that although no significant trend over time was detected in maturation reaction
428 norms of Barents Sea haddock, strong selection may have been present earlier: fishing

429 mortality in the 1950s was approximately double that of recent years and has steadily declined
430 (see Fig. 1e). In the thirty years prior to sampling, adaptation to fishing pressure may have
431 occurred; such rapid adaptation to anthropogenic disturbances, over the time span of a few
432 generations of the organism, has been increasingly reported (Kinnison and Hendry, 2001;
433 Hendry et al., 2008; Darimont et al., 2009). Adaptation to past exploitation could have led to a
434 situation in which selection during the study period was absent or too weak to cause
435 significant evolutionary change. Variation and reversals in evolutionary trajectories is
436 common in many contemporary evolution and paleontological studies (Hendry and Kinnison,
437 1999), and recent experimental work by Conover et al. (2009) suggests that harvested
438 populations possess the ability to recover from the fisheries-induced evolution. The last
439 scenario, that we were unable to detect a change that actually took place, could also apply
440 because several challenges in estimating representative population parameters for this stock
441 existed – primarily as a result of behavioural changes (and resultant gear selectivity issues)
442 and emigration from the study area. Nevertheless, we conclude that the most parsimonious
443 interpretation of our results from the Barents Sea haddock is that maturation in this population
444 has not evolved during the study period.

445 **5. Conclusions**

446 Changes in maturation of Barents Sea haddock were investigated and multiple potential
447 drivers examined included exploitation, water temperature, salinity, the North Atlantic
448 Oscillation, species interactions, and density dependent effects. No significant temporal trends
449 in maturation exist for the 1983–2003 cohorts, and we could not find evidence for
450 exploitation driving changes in maturation. Instead, water temperature and salinity appeared
451 to be the most important variables tested that explained the variation in maturation for both
452 sexes, on top of the effects of age and length. Possible reasons for the lack of trend suggestive

453 of fisheries-induced evolution may be that we were unable to detect a change given the
454 challenges in estimating sampling parameters, that adaptation to higher exploitation in the
455 past resulted in negligible evolutionary selection during the study period when exploitation
456 has been more moderate, or that change in the trait is in a period of stasis or reversal.

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465

466 **Appendix A. Supplementary data**

467

468 **References**

469 Aglen, A., Alvsvåg, J., Grekov, A., Høines, Å., Mehl, S., Zhukova, N., 2005. Investigations
470 of demersal fish in the Barents Sea winter 2005. IMR/PINRO Joint Report Series, No.
471 4/2005, p. 58.

472 Aglen, A., Alvsvåg, J., Høines, Å., Johannesen, E., Mehl, S., 2008. Investigations on
473 demersal fish in the Barents Sea winter 2006. IMR/PINRO Joint Report Series, No.
474 13/2008, p. 52.

475 Aglen, A., Drevetnyak, K., Jakobsen, T., Korsbrekke, K., Lepesevich, Y., Mehl, S., Nakken,
476 O., Nedreaas, K.H., 2000. Investigations of demersal fish in the Barents Sea winter 2000.
477 IMR/PINRO Joint Report Series. No. 5/2001, p. 74.

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

480 Bates, D.M., Maechler, M., 2010. lme4: Linear mixed-effects models using S4 classes. R
481 package version 0.999375-37.

482 Baulier, L., Heino, M., Lilly, G.R., Dieckmann, U., 2006. Body condition and evolution of
483 maturation of Atlantic cod in Newfoundland. *ICES CM* 2006/H:19.

484 Bochkov, Y.A., 1982. Water temperature in the 0-200m layer in the Kola-Meridian in the
485 Barents Sea, 1900-1981. *SB Nauchn Trud PINRO* 46, 113-122 (In Russian).

486 Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H.,
487 White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and
488 evolution. *Trends Ecol. Evol.* 24, 127-135.

489 Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference*. Springer-
490 Verlag, New York.

491 Conover, D.O., Arnott, S.A., Walsh, M.R., Munch, S.B., 2005. Darwinian fishery science:
492 lessons from the Atlantic silverside (*Menidia menidia*). *Can. J. Fish. Aquat. Sci.* 62, 730-
493 737.

494 Conover, D.O., Munch, S.B., 2002. Sustaining fisheries yields over evolutionary time scales.
495 *Science* 297, 94-96.

496 Conover, D.O., Munch, S.B., Arnott, S.A., 2009. Reversal of evolutionary downsizing caused
497 by selective harvest of large fish. *Proc. R. Soc. Lond. B* 276, 2015-2020.

498 Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E., Wilmers, C.C.,
499 2009. Human predators outpace other agents of trait change in the wild. Proc. Natl. Acad.
500 Sci. USA 106, 952-954.

501 Demidenko, E., 2004. Mixed models: theory and applications. Wiley-Interscience, Hoboken,
502 N.J.

503 Devold, F., 1938. The North Atlantic halibut and net fishing. Fiskeridirektoratets Skrifter
504 Serie Havundersøkelser 5, 1-47.

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

507 Froese, R., Binohlan, C., 2000. Empirical relationships to estimate asymptotic length, length
508 at first maturity and length at maximum yield per recruit in fishes, with a simple method
509 to evaluate length frequency data. J. Fish. Biol. 56, 758-773.

510 Gjørseter, J., Loeng, H., 1987. Growth of the Barents Sea capelin, *Mallotus villosus*, in
511 relation to climate. Environ. Biol. Fish. 20, 293-300.

512 Grift, R.E., Heino, M., Rijnsdorp, A.D., Kraak, S.B.M., Dieckmann, U., 2007. Three-
513 dimensional maturation reaction norms for North Sea plaice. Mar. Ecol. Prog. Ser. 334,
514 213-224.

515 Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M., Dieckmann, U., 2003. Fisheries-induced
516 trends in reaction norms for maturation in North Sea plaice. Mar. Ecol. Prog. Ser. 257,
517 247-257.

518 Halliday, R.G., Cooper, C.G., Fanning, P., Hickey, W.M., Gagnon, P., 1999. Size selection of
519 Atlantic cod, haddock and pollock (saithe) by otter trawls with square and diamond mesh
520 codends of 130-155 mm mesh size. Fish. Res. 41, 255-271.

521 Heino, M., Dieckmann, U., 2008. Detecting fisheries-induced life-history evolution: an
522 overview of the reaction norm approach. Bull. Mar. Sci. 83, 69-93.

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

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

528 Heino, M., Dieckmann, U., Godø, O.R., 2002c. Reaction norm analysis of fisheries-induced
529 adaptive change and the case of the Northeast Arctic cod. *ICES CM 2002/Y:14*, p. 14.

530 Hendry, A., Farrugia, T.J., Kinnison, M., 2008. Human influences on rates of phenotypic
531 change in wild animal populations. *Mol. Ecol.* 17, 20-29.

532 Hendry, A.P., Kinnison, M.T., 1999. Perspective: the pace of modern life: measuring rates of
533 contemporary microevolution. *Evolution* 53, 1637-1653.

534 Hurrell, J.W., Deser, C., 2009. North Atlantic climate variability: The role of the North
535 Atlantic Oscillation. *J. Marine Systems* 78, 28-41.

536 Hurrell, J.W., Dickson, R.R., 2004. Climate variability over the North Atlantic. In: Stenseth,
537 N.C., Ottersen, G., Hurrell, J.W., Belgrano, A. (Eds.). *Marine Ecosystems and Climate*
538 *Variation - the North Atlantic*. Oxford University Press, Oxford, p. 252.

539 Huse, I., Løkkeborg, S., Soldal, A.V., 2000. Relative selectivity in trawl, longline and gillnet
540 fisheries for cod and haddock. *ICES J. Mar. Sci.* 57, 1271-1282.

541 ICES, 2008. 2008 Report of the ICES Advisory committee. *ICES Advice, 2008*. Book 3. p.
542 106.

543 ICES, 2009. Report of the Arctic Fisheries Working Group (AFWG), 21-27 April 2009, San-
544 Sebastian, Spain. *ICES CM 2009\ACOM:02*. ICES, Copenhagen, p. 588.

545 ICES, 2010. Report of the Arctic Fisheries Working Group (AFWG), 22-28 April 2010,
546 Lisbon, Portugal/Bergen, Norway. *ICES CM 2010-ACOM:05*. ICES, Copenhagen, p.
547 664.

548 Ingvaldsen, R., Loeng, H., Ådlandsvik, B., Stiansen, J.E., 2006. Økosystem Barentshavet:
549 fysikk. In: Iversen, S. (Ed.). *Havets Ressurser og Miljø*. Havforskningsinstituttet, Fiskeri
550 og havet, særnummer 1-2006. Bergen, pp. 20-23 (In Norwegian with English summaries
551 and figure captions).

552 Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande,
553 B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka,
554 A., Dieckmann, U., Heino, M., Rijnsdorp, A.D., 2007. Ecology: Managing Evolving Fish
555 Stocks. *Science* 318, 1247-1248.

556 Kinnison, M.T., Hendry, A.P., 2001. The pace of modern life II: from rates of contemporary
557 microevolution to pattern and process. *Genetica* 112-113, 145-164.

558 Korsbrekke, K., 1999. Variations in maturity of haddock in the Barents Sea in relation to
559 year-class strength, age, size, sex and area. *J. Northw. Atl. Fish. Sci.* 25, 37-45.

560 Korsbrekke, K., 2003. Some aspects of estimating proportions mature and potential
561 implications for stock predictions. In: Kjesbu, O.S., Hunter, J.R., Witthames, P.R. (Eds.).
562 Report of the Working Group on Modern approaches to assess maturity and fecundity of
563 warm-and cold-water fish and squids, Bergen, Norway, 4-7 September 2001, pp. 89-98.

564 Kovtsova, M.V., 1993. Growth rate and maturation of Arcto-Norwegian haddock in 1987-
565 1990. ICES CM 1993/G:58.

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

567 Loeng, H., Ozhigin, V.K., Ådlandsvik, B., 1997. Water fluxes through the Barents Sea. *ICES*
568 *J. Mar. Sci.* 54, 310-317.

569 Manly, F.J., 1991. Randomization, bootstrap and Monte Carlo methods in biology. Chapman
570 and Hall, London.

571 Miller, R.B., 1957. Have the genetic pattern of fishes been altered by introductions or by
572 selective fishing? *J. Fish. Res. Bd. Can.* 14, 797-806.

573 Mollet, F.M., Kraak, S.B.M., Rijnsdorp, A.D., 2007. Fisheries-induced evolutionary changes
574 in maturation reaction norms in North Sea sole *Solea solea*. Mar. Ecol. Prog. Ser. 351,
575 189-199.

576 Nelson, K., Soulé, M., 1987. Genetical conservation of exploited fishes. In: Ryman, N., Utter,
577 F. (Eds.). Population genetics & fishery management. Washington Sea Grant Program,
578 Seattle, pp. 345-368.

579 Neuheimer, A.B., Taggart, C.T., 2010. Can changes in length-at-age and maturation timing in
580 Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing? Can. J.
581 Fish. Aqu. Sci. 67, 854-865.

582 Olsen, E., Aanes, S., Mehl, S., Holst, J.C., Aglen, A., Gjørseter, J., 2010. Cod, haddock,
583 saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the
584 biological value of the area. ICES J. Mar. Sci. 67, 87-101.

585 Ottersen, G., Loeng, H., 2000. Covariability in early growth and year-class strength of
586 Barents Sea cod, haddock, and herring: the environmental link. ICES J. Mar. Sci. 57, 339-
587 348.

588 Ottersen, G., Stenseth, N.C., 2001. Atlantic climate governs oceanographic and ecological
589 variability in the Barents Sea. Limnol. Oceanogr. 46, 1774-1780.

590 Pardoe, H., Vainikka, A., Thórdarson, G., Marteinsdottir, G., Heino, M., 2009. Temporal
591 trends in probabilistic maturation reaction norms and growth of Atlantic cod (*Gadus*
592 *morhua*) on the Icelandic shelf. Can. J. Fish. Aquat. Sci. 66, 1719-1733.

593 Pennington, M., Vølstad, J.H., 1994. Assessing the effect of intra-haul correlation and
594 variable density on estimates of population characteristics from marine surveys.
595 Biometrics 50, 725-732.

596 Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects models in S and S-PLUS. Springer, New
597 York.

598 Reznick, D.A., Bryga, H., Endler, J.A., 1990. Experimentally induced life-history evolution in
599 a natural population. *Nature* 346, 357-359.

600 Reznick, D.A., Ghalambor, C.K., 2005. Can commercial fishing cause evolution? Answers
601 from guppies (*Poecilia reticulata*). *Can. J. Fish. Aquat. Sci.* 62, 791-801.

602 Ricker, W.E., 1981. Changes in the average size and average age of Pacific salmon. *Can. J.*
603 *Fish. Aquat. Sci.* 38, 1636-1656.

604 Rijnsdorp, A.D., 1993a. Fisheries as a large-scale experiment on life-history evolution:
605 disentangling phenotypic and genetic effects in changes in maturation and reproduction of
606 North Sea plaice, *Pleuronectes platessa* L. *Oecologia* 96, 391-401.

607 Rijnsdorp, A.D., 1993b. Relationship between juvenile growth and the onset of sexual
608 maturity of female North Sea plaice, *Pleuronectes platessa*. *Can. J. Fish. Aquat. Sci.* 50.

609 Rijnsdorp, A.D., Grift, R.E., Kraak, S.B.M., 2005. Fisheries-induced adaptive change in
610 reproductive investment in North Sea plaice (*Pleuronectes platessa*)? *Can. J. Fish. Aquat.*
611 *Sci.* 62, 833-843.

612 Rollefson, G., 1933. The otoliths of the cod. *Fiskeridirektoratets Skrifter Serie*
613 *Havundersøkelser* 4, 1-18.

614 Schauer, U., Loeng, H., Rudels, B., Ozhigin, V.K., Dieck, W., 2002. Atlantic water flow
615 through the Barents and Kara Seas. *Deep-Sea Res. Pt. I* 49, 2281-2298.

616 Sharpe, D.M.T., Hendry, A., 2009. Life history change in commercially exploited fish stocks:
617 an analysis of trends across studies. *Evol. Appl.* 2, 260-275.

618 Silliman, R., 1975. Selective and unselective exploitation of experimental populations of
619 *Tilapia mossambica*. *Fish. Bull.* 73, 495-507.

620 Smith, G.M., Ieno, E.N., Saveliev, A.A., Walker, N., Zuur, A.F., 2009. Mixed effects models
621 and extensions in ecology with R. Springer-Verlag New York, New York, NY.

- 622 Solemdal, P., Knutsen, T., Bjørke, H., 1989. Spawning areas and spawning period of the
623 north-east Arctic haddock (*Melanogrammus aeglefinus* L.). Havforskningsinstituttets egg-
624 og larveprogram (HELP), Nr. 25, p. 43.
- 625 Stiansen, J.E., Aglen, A., Bogstad, B., Budgell, P., Dalpadado, P., Dolgov, A.V., Dommasnes,
626 A., Filin, A.A., Gjørseter, H., Hauge, K.H., Høines, Å., Ingvaldsen, R., Johannessen, A.,
627 Jørgensen, L.L., Karsakov, A.L., Klungsøyr, J., Knutsen, T., Lien, V., Loeng, H., Mehl,
628 S., Mortensen, P.B., Muchina, N.V., Nesterova, V.N., Olsen, E., Orlova, E.L., Ozhigin,
629 V.K., Pedchenko, A.P., Stenevik, E.K., Skogen, M., Titov, O.V., Tjelmeland, S.,
630 Zabavnikov, V.B., Ziryanov, S.V., Zhukova, N.G., Øien, N., Aanes, S., 2005. Joint
631 PINRO/IMR report on the state of the Barents Sea ecosystem 2005/2006. IMR/PINRO
632 Joint Report Series No. 3/2006, p. 122.
- 633 Stokes, T.K., McGlade, J.M., Law, R., 1993. The exploitation of evolving resources.
634 Springer-Verlag, Berlin.
- 635 Swain, D.P., 2011. Life-history evolution and elevated natural mortality in a population of
636 Atlantic cod (*Gadus morhua*). *Evol. Appl.* 4, 18-29.
- 637 Templeman, W., Hodder, V.M., Wells, R., 1978. Sexual maturity and spawning in haddock,
638 *Melanogrammus aeglefinus*, of the southern Grand Bank. *Res Bull ICNAF* No. 13, pp. 53-
639 65.
- 640 Thomas, G., Quoss, H., Hartmann, J., Eckmann, R., 2009. Human-induced changes in the
641 reproductive traits of Lake Constance common whitefish (*Coregonus lavaretus*). *J. Evol.*
642 *Biol.* 22, 88-96.
- 643 Tobin, D., Wright, P.J., O'Sullivan, M., 2010. Timing of the maturation transition in haddock
644 *Melanogrammus aeglefinus*. *J. Fish. Biol.* 77, 1252-1267.

645 Uusi-Heikkilä, S., Kuparinen, A., Wolter, C., Meinelt, T., O'Toole, A.C., Arlinghaus, R.,
646 2011. Experimental assessment of the probabilistic maturation reaction norm: condition
647 matters. *Proc. R. Soc. Lond. B* 278, 709-717.

648 Vainikka, A., Gårdmark, A., Bland, B., Hjelm, J., 2009a. Two- and three-dimensional
649 maturation reaction norms for the eastern Baltic cod, *Gadus morhua*. *ICES J. Mar. Sci.*
650 66, 248-257.

651 Vainikka, A., Mollet, F., Casini, M., Gårdmark, A., 2009b. Spatial variation in growth,
652 condition and maturation reaction norms of the Baltic herring *Clupea harengus membras*.
653 *Mar. Ecol. Prog. Ser.* 383, 285-294.

654 van Walraven, L., Mollet, F.M., van Damme, C.J.G., Rijnsdorp, A.D., 2010. Fisheries-
655 induced evolution in growth, maturation and reproductive investment of the sexually
656 dimorphic North Sea plaice (*Pleuronectes platessa* L.). *J. Sea Res.* 64, 85-93.

657 Wang, H., Höök, T.O., Ebener, M.P., Mohr, L.C., Schneeberger, P.J., 2008. Spatial and
658 temporal variation of maturation schedules of lake whitefish (*Coregonus clupeaformis*) in
659 the Great Lakes. *Can. J. Fish. Aquat. Sci.* 65, 2157-2169.

660 Wright, P.J., 2007. Understanding the maturation process for field investigations of fisheries-
661 induced evolution. *Mar. Ecol. Prog. Ser.* 335, 279-283.

662

663

664 Legends

665 **Table 1**

666 Results of GLMM and GLM models and sensitivity tests (GLMM models only) for the direct
667 PMRN method. The p-value is from the likelihood ratio test between the no environmental
668 term model and the model including the environmental term, and coefficient expl. 1 and expl.
669 2 refer to the coefficients for the environmental terms. Model term abbreviations are: L =
670 length, A = age, C = cohort, A:C is the age×cohort interaction, L:A = length×age interaction
671 term, VNT.2 = Vardø North water temperature lagged 2 years, FBT.1 = Fugløy-Bear Island
672 water temperature lagged 1 year, and KS.2 is salinity from the Kola transect lagged 2 years.

673 **Fig. 1**

674 Standardized plots of explanatory variables used in the analysis: (a) water temperature from
675 the Kola transect, Fugløy-Bear Island (FB) transect, and Vardø-North section (VN); (b)
676 salinity from the Kola and Fugløy-Bear Island (FB) transect; (c) NAO index; (d) biomass of
677 cod, capelin and haddock; and (e) capelin:cod biomass ratio, and haddock fishing mortality
678 averaged for ages 3-7 and 3-11.

679 **Fig. 2**

680 Mean length and standard deviation of male and female haddock by age and cohort. Black
681 circles represent mature fish, open (grey) circles are immature fish.

682 **Fig. 3**

683 Temporal trend in the reaction norm for size and age at maturation midpoints for male and
684 female haddock. Black circles represent GLMM model estimates, grey circles are GLM
685 estimates (open grey circles are the one-term GLM model). Vertical bars are the bootstrapped
686 95% confidence intervals of the estimates.

Table 1

Model		AIC/ QAIC	Deviance	Random effects: σ^2	p-value	Coefficient Expl. 1	Coefficient Expl. 2
Males							
(1) L + A + C + A:C	GLMM	3398	3310	3.29			
(2) L + A + C + A:C + VNT.2	GLMM	3390	3300	3.21	< 0.001	1.18	
(1) L + A + C + A:C	GLM	7079	3553	–			
(2) L + A + C + A:C + VNT.2	GLM	6966	3534	–	< 0.001	1.06	
Model (2) without down-weighting	GLMM	3998	3908	9.56		1.36	
Model (2) without survey area weighting	GLMM	4117	4027	12.47		1.47	
Model (2) without any weighting	GLMM	4777	4687	29.20		2.00	
Females							
(3) L + A + C + L:A	GLMM	2782	2732	3.31			
(4) L + A + C + L:A + FBT.1	GLMM	2773	2721	3.22	< 0.001	0.84	
(5) L + A + C + L:A + KS.2	GLMM	2768	2716	3.33	< 0.001		-0.67
(6) L + A + C + L:A + FBT.1 + KS.2	GLMM	2758	2704	3.25	< 0.001	0.86	-0.68
(3) L + A + C + L:A	GLM	5402	2945	–			
(4) L + A + C + L:A + FBT.1	GLM	5505	2928	–	< 0.001	0.67	
(5) L + A + C + L:A + KS.2	GLM	5266	2926	–	< 0.001		-0.46
(6) L + A + C + L:A + FBT.1 + KS.2	GLM	5333	2909	–	< 0.001	0.68	-0.47
Model (6) without down-weighting	GLMM	3238	3184	7.92		0.97	-0.85
Model (6) without survey area weighting	GLMM	3436	3382	11.34		0.92	-0.92
Model (6) without any weighting	GLMM	4004	3950	23.46		1.00	-1.16

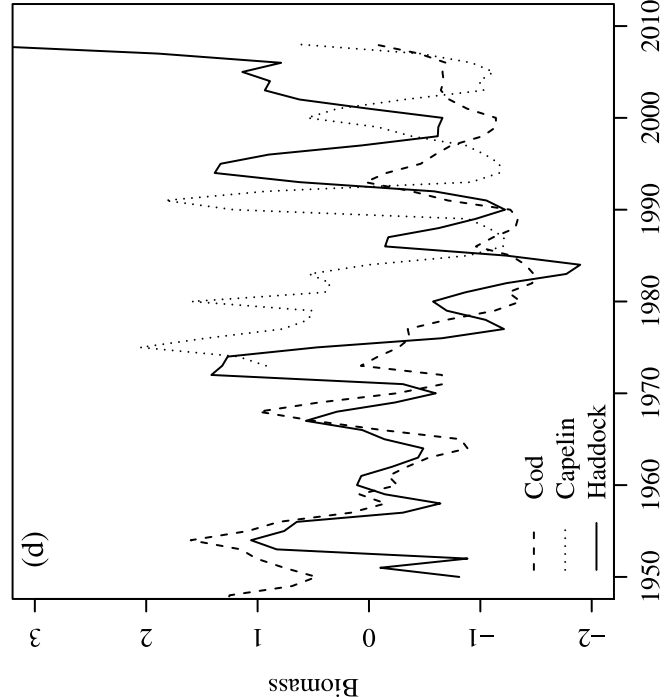
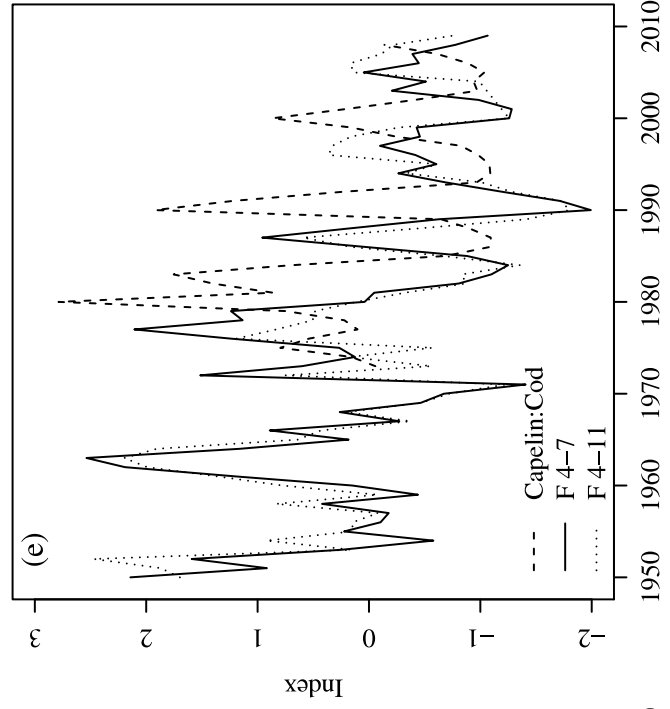
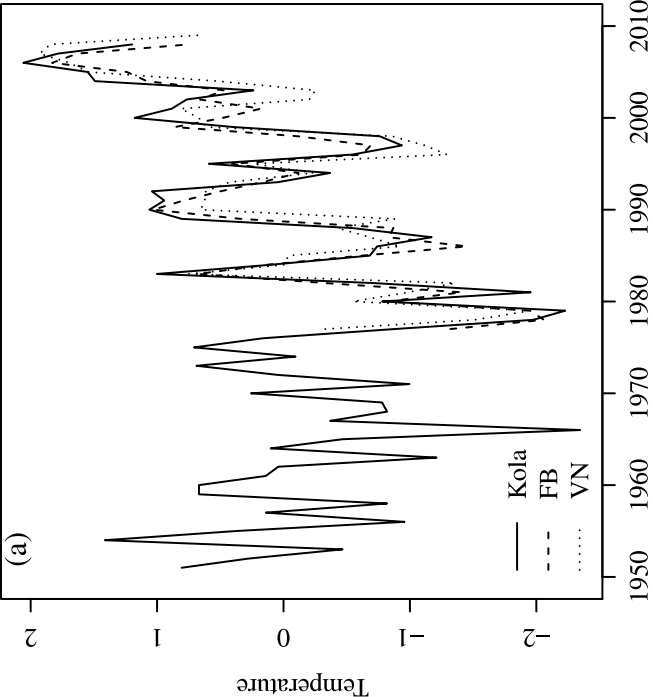
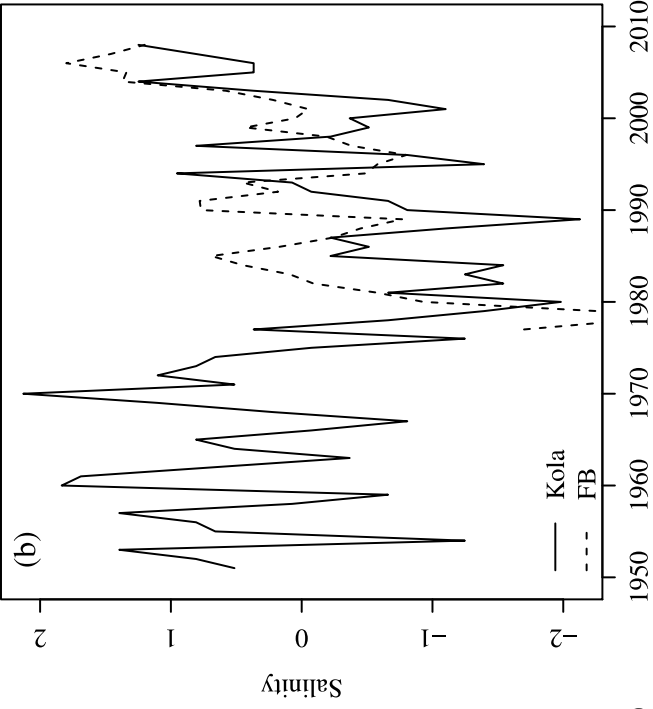
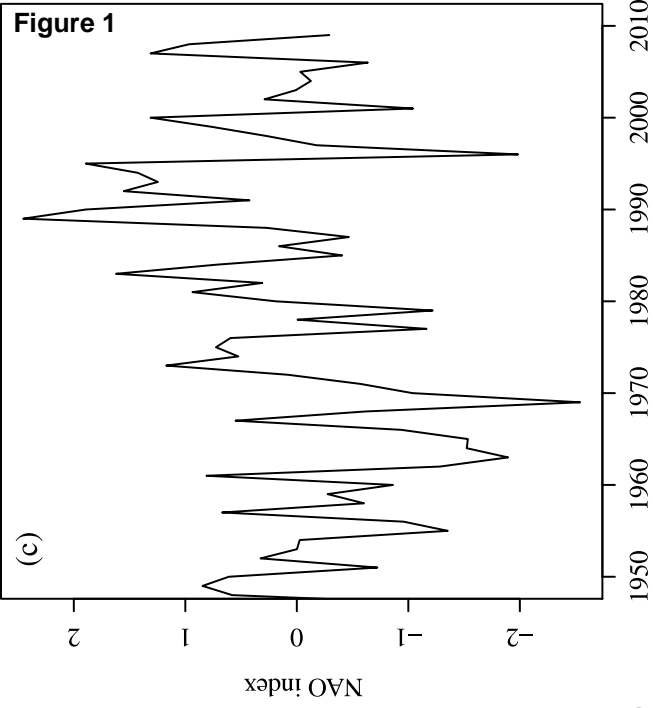


Figure 2

