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## Interim Report

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### **Assessing Changes in Age and Size at Maturation in Collapsing Populations of Atlantic Cod (*Gadus morhua*)**

Esben Moland Olsen (e.m.olsen@bio.uio.no)  
George R. Lilly (lillyg@dfo-mpo.gc.ca)  
Mikko Heino (mikko.heino@imr.no)  
M. Joanne Morgan (morganj@dfo-mpo.gc.ca)  
John Brattey (bratteyj@dfo-mpo.gc.ca)  
Ulf Dieckmann (dieckmann@iiasa.ac.at)

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#### **Approved by**

Leen Hordijk  
Director, IIASA

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1    **Assessing changes in age and size at maturation in collapsing populations of**  
2    **Atlantic cod (*Gadus morhua*)**

3

4    **Esben Moland Olsen<sup>1,2,5</sup>, George R. Lilly<sup>3</sup>, Mikko Heino<sup>1,4</sup>, M. Joanne Morgan<sup>3</sup>, John**  
5    **Brattey<sup>3</sup>, and Ulf Dieckmann<sup>1</sup>**

6

7    <sup>1</sup> *Adaptive Dynamics Network, International Institute for Applied Systems Analysis (IIASA),*  
8    *A-2361 Laxenburg, Austria*

9    <sup>2</sup> *Present address: Centre for Ecological and Evolutionary Synthesis, Department of Biology,*  
10    *University of Oslo, P.O. Box 1050, Blindern, N-0316 Oslo, Norway*

11    <sup>3</sup> *Northwest Atlantic Fisheries Centre, Department of Fisheries and Oceans, P.O. Box 5667,*  
12    *St. John's, Newfoundland, Canada, A1C 5X1*

13    <sup>4</sup> *Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway*

14    <sup>5</sup> *Corresponding author*

26   **Abstract:** By estimating probabilistic reaction norms for age and size at maturation, we  
27   show that maturation schedules of Atlantic cod (*Gadus morhua*) off Labrador and  
28   Newfoundland shifted toward earlier ages and smaller sizes during the late 1980s and early  
29   1990s, when these populations underwent a severe collapse in biomass and subsequently were  
30   closed for directed commercial fishing. We also demonstrate that this trend towards  
31   maturation at younger ages and smaller sizes is halted and even shows signs of reversal  
32   during the closure of the fisheries. In addition, our analysis reveals that males tend to mature  
33   earlier and at a smaller size than females, and that maturation age and size decreases with  
34   increasing latitude. Importantly, the maturation reaction norms presented here are robust to  
35   variation in survival and growth (through phenotypic plasticity), and are thus strongly  
36   indicative of rapid evolutionary changes in cod maturation, as well as of spatial and sex-  
37   specific genetic variation. We therefore suggest that maturation reaction norms can provide  
38   helpful reference points for managing harvested populations with evolving life-histories.

39

40   Keywords: *evolution, fisheries, Gadus morhua, maturation reaction norms, phenotypic*  
41   *plasticity*

42     **Introduction**

43       There is accumulating evidence that significant evolutionary changes may occur on  
44       contemporary timescales in natural populations, often within just a few years or decades  
45       (Reznick et al. 1990; Hendry et al. 2000; Grant and Grant 2002). In some cases such changes  
46       may be brought about by single episodes of particularly strong selection. For instance, the  
47       beak size of Darwin's finches (*Geospiza fortis*) on the Galapagos Islands evolved in response  
48       to a drought episode occurring within the timescale of one generation (Grant and Grant 2002).  
49       In the light of these findings, it has recently been argued that microevolution should be  
50       accounted for in the management of harvested populations and, more generally, in  
51       conservation biology (Stokes and Law 2000; Stockwell et al. 2003; Ferrière et al. 2004).

52       The populations of Atlantic cod (*Gadus morhua*) found off Labrador and Newfoundland  
53       in the Northwest Atlantic supported rich fisheries for hundreds of years (Templeman 1966;  
54       Hutchings and Myers 1995), but suffered a major decline in the early 1970s and a collapse in  
55       the late 1980s to early 1990s (Taggart et al. 1994; Myers et al. 1997). This collapse forced the  
56       Canadian government to close down much of the cod fisheries, and many coastal  
57       communities that used to depend on the cod experienced much economic and social hardship  
58       (Felt and Locke 1995). The moratorium on cod fishing has remained in effect in the areas that  
59       used to support the largest catches of cod (Lilly et al. 2003).

60       Evolutionary theory predicts that the heavy mortality imposed by industrial fisheries may  
61       cause evolutionary changes in exploited fish populations (Law and Grey 1989; Policansky  
62       1993; Abrams and Rowe 1996). Especially, an increase in mortality at potential ages and sizes  
63       at maturation is expected to select for an earlier onset of maturation (Charlesworth 1994;  
64       Taborsky et al. 2003; Ernande et al. 2004). Specifically, it has been hypothesized that the  
65       collapse of the Canadian cod populations was a major selective episode strongly favouring  
66       early-maturing genotypes relative to late-maturing genotypes (Hutchings 1999).

67 Yet, detecting contemporary evolution in the wild is a major challenge. It requires that  
68 genetic changes are successfully identified among the total phenotypic variation. Expressed  
69 life-history traits will be influenced not only by genetics, but also by environmental variation  
70 through phenotypic plasticity. Harvested fish populations typically show trends towards an  
71 increased percentage of mature individuals at younger ages and smaller sizes; the Canadian  
72 cod populations being no exception (Trippel 1995). While these changes could reflect genetic  
73 responses to fishing mortality (Law and Grey 1989; Heino 1998; Heino and Godø 2002), they  
74 may also result, through phenotypic plasticity, from increased resource availability and faster  
75 growth of survivors after stock biomass has been depleted. Faster-growing individuals will  
76 often mature at an earlier age than slower-growing individuals (Alm 1959). Because of such  
77 confounding effects, the nature of phenotypic changes in exploited fish populations is not yet  
78 well understood (Law 2000).

79 Maturation reaction norms can shed new light on the relative roles of environmental  
80 fluctuations and genetic changes as causes of variation in maturation patterns (Heino et al.  
81 2002a). By definition, a reaction norm describes the phenotypes expressed by a genotype  
82 under different environmental conditions (Schmalhausen 1949). Stearns and Koella (1986)  
83 used variation in somatic growth as a surrogate for variation in environmental conditions  
84 when modeling reaction norms for age and size at maturation. A recently developed  
85 probabilistic extension of this reaction norm approach (Heino et al. 2002a) models the  
86 maturation process based on the probability that individuals having reached a given age and  
87 size mature in the next season. By construction, this probability is independent of variations in  
88 growth and survival that determine the likelihood that individuals reach a given age and size  
89 (Heino et al. 2002a). Hence, the probabilistic reaction norm approach is useful for detecting  
90 changes in maturation, without being confounded by changes in growth and survival, and can  
91 thereby help to disentangle the effects of phenotypic plasticity and of genetic variation on

92 maturation. (see *Materials and Methods: Maturation reaction norms*). The probabilistic  
93 maturation reaction norm terminology assumes that variation growth is mainly  
94 environmentally determined (see *Discussion*).

95 For management purposes, it is important to be able to detect changes in life histories in  
96 exploited populations as early as possible. There are several reasons for this need. First, rapid  
97 evolutionary life-history responses caused by experimental harvesting that mimics fishing  
98 (removal of larger individuals) have been shown to cause a significant reduction in  
99 harvestable biomass (Conover and Munch 2002). Second, in Atlantic cod and in many other  
100 species of fish, young females are known to breed for a shorter period, produce fewer egg  
101 batches, exhibit lower fecundity, and produce smaller eggs with lower fertilization and  
102 hatching rates, compared to older spawners (Trippel 1998; Berkeley et al. 2004a). Third, it is  
103 important to understand the underlying causes of changes in life histories, in particular,  
104 whether these are mainly due to phenotypic plasticity or genetics. While plastic changes are in  
105 principle easily reversible, this may not be the case for genetic changes. Fourth, detecting life-  
106 history changes at an early stage may aid managers by providing important additional clues  
107 about the status of a population. While population size is often the variable of focal interest  
108 for managers, it can be very difficult to detect changes in the abundance of populations in the  
109 wild. In oceanic fish populations uncertainties in harvest statistics are typically large, and the  
110 same applies to population abundance surveys (Trippel 1995; Myers et al. 1997). An observed  
111 shift toward earlier maturation could then serve as a “stress” indicator (Trippel 1995).

112 In this study, we employ the new method of estimating probabilistic reaction norms for  
113 age and size at maturation to Atlantic cod (*Gadus morhua*) populations found off Labrador  
114 and Newfoundland in the Northwest Atlantic. We characterize the maturation process in the  
115 years prior to, during, and after the dramatic collapse of these populations in the late 1980s  
116 and early 1990s, independently of temporal changes in growth and survival rates, and thereby

117 provide new insights about the biology of these stocks, as well as about the relative roles of  
118 environmental fluctuations and genetic changes as causes of changing maturation patterns.  
119 Previously, we have estimated maturation reaction norms for female cod from off southern  
120 Labrador and eastern Newfoundland (Olsen et al. 2004), finding evidence for maturation  
121 reaction norms having shifted toward earlier ages and smaller sizes during the stock collapse,  
122 which strongly suggests that an evolutionary response to high fishing pressure took place in  
123 this period. Here, we expand on these findings by comparing the maturation reaction norms of  
124 both female and male cod sampled from a broader geographic area. We also discuss how  
125 reaction norms for age and size at maturation may serve as biological indicators, or reference  
126 points, for the management of harvested populations.

127

## 128 **Materials and Methods**

### 129 **Northern (2J3KL) cod**

130 The designation ‘northern cod’ refers to Atlantic cod found off southern Labrador  
131 (Northwest Atlantic Fisheries Organization ,NAFO, Division 2J) through the Northeast  
132 Newfoundland Shelf (Division 3K) to the northern half of the Grand Bank off eastern  
133 Newfoundland (Division 3L, Fig. 1). Northern cod is probably structured into several  
134 (sub)populations (Templeman 1966; Ruzzante et al. 1998; Beacham et al. 2002).

135 The collapse in the late 1980s and early 1990s reduced the cod abundance to about 2% of  
136 that in the early 1980s (Taggart et al. 1994; Myers et al. 1997; Lilly et al. 2003). There has  
137 been much controversy about the relative importance of fishing mortality, natural mortality,  
138 and emigration as causes of the collapse. Some argue that fishing was by far the most  
139 important driving factor (Hutchings and Myers 1994; Hutchings 1996; Myers et al. 1996).  
140 Others suggest that a spectrum of environmental factors, both abiotic and biotic, changed  
141 during the period of stock collapse; these factors may have increased the natural mortality of

142 cod, as well as induced shifts in its geographical distribution (Baird et al. 1992; deYoung and  
143 Rose 1993; Kulka et al. 1995). Still, there is broad agreement that increased fishing mortality  
144 was an important factor in the collapse (Rose et al. 2000; Smedbol et al. 2002).

145 In July 1992, the Canadian government declared a moratorium on directed fishing of  
146 northern cod. This moratorium has remained in effect in the offshore, but was lifted for a few  
147 years (1998-2002) to allow a small fishery in the inshore (Lilly et al. 2003). Despite the  
148 moratorium, northern cod has not recovered, and its estimated population biomass remains at  
149 an historically low level (Lilly et al. 2003). There are several hypotheses as to why northern  
150 cod has not recovered; these include by-catches in fisheries directed at other species (Lilly et  
151 al. 2003), poor food availability (Rose and O'Driscoll 2002); increased predation from harp  
152 seals (Bundy 2001); various Allee effects (Frank and Brickman 2000; De Roos and Persson  
153 2002; Rowe and Hutchings 2003); predation by other fish on cod eggs, larvae, and very early  
154 juveniles (Swain and Sinclair 2000; Walters and Kitchell 2001); and reductions in the  
155 reproductive potential of the spawning fish (Trippel 1995; Anderson and Rose 2001). The last  
156 hypothesis is inspired by the low number of spawning individuals and the truncated age-  
157 distribution now characterizing the northern cod populations (Lilly et al. 2003).

158

### 159 **Southern Grand Bank (3NO) cod**

160 Cod in NAFO Divisions 3NO inhabit the southern Grand Bank of Newfoundland (Fig. 1).  
161 Like northern cod, the 3NO cod populations suffered a major decline in biomass in the late  
162 1980s and early 1990s (Myers et al. 1997; Healey et al. 2003). The population structure of  
163 3NO cod is not rigorously defined, and some seasonal mixing with cod in subdivision 3Ps  
164 may occur (Healey et al. 2003). A moratorium on directed fishing of 3NO cod was imposed in  
165 February 1994, and has remained in effect since. Despite this effort, 3NO cod also has not

166 recovered (Healey et al. 2003). It is suggested that by-catch of cod in other fisheries has  
167 increased to a point where it is impeding stock recovery (Healey et al. 2003).

168

169 **St. Pierre Bank (3Ps) cod**

170 Cod in NAFO Subdivision 3Ps is found south of Newfoundland, on and around the St.  
171 Pierre Bank (Fig. 1). The population structure of 3Ps cod is not well defined, and the stock is  
172 considered a complex mixture of sub-components. The abundance of 3Ps cod decreased  
173 substantially in the late 1980s and early 1990s, although the collapse was not as dramatic as  
174 for northern cod or for southern Grand Bank cod (Myers et al. 1997; Lilly et al. 2003). The  
175 3Ps cod stock was under a moratorium from August 1993 to 1997, and population sizes have  
176 – in marked contrast to northern cod and southern Grand Bank cod –rebuilt to a considerable  
177 extent since the collapse (Brattey et al. 2003).

178

179 **Analyzed data**

180 We analyzed data on Atlantic cod caught in stratified random bottom-trawl surveys  
181 conducted annually by the Canadian Department of Fisheries and Oceans (DFO). Autumn  
182 surveys cover the distribution range of northern cod (2J3KL), while the data on cod from the  
183 southern Grand Bank (3NO) and the St. Pierre Bank (3Ps) are mainly from spring surveys.  
184 There is also a spring survey on northern cod from the 3L Division. The autumn surveys are  
185 normally conducted during October to November and the spring surveys usually during April  
186 to May. The autumn survey was initiated in Division 2J and 3K in 1977, and in Division 3L in  
187 1981. The spring survey was initiated in Division 3L, 3N, and 3O in 1971, and in Division  
188 3Ps in 1972. Age and maturity sampling of captured cod was stratified by fish body length  
189 (Shelton et al. 1999; Lilly et al. 2003). Cod were aged on the basis of otoliths that contain  
190 annual rings reflecting a fish's seasonal growth pattern (Rollefsen 1933). Sex and maturity

191 status were determined by visual inspection of the gonads. Body length was measured to the  
192 nearest cm. Age is here expressed as if the cod were sampled on their nominal birthday  
193 (January 1), which required adding one year to the ages from the autumn survey. Further  
194 details about sampling procedures and data are given by Lilly et al. (2003), Brattey et al.  
195 (2003), and Healey et al. (2003).

196 All cod of age 1 and 2 years were juvenile and were not included in the analyses. These  
197 youngest age-classes were also poorly represented in the samples due to the sampling device  
198 used (Lilly et al. 2003). Note that the Engel trawl used for sampling the cod was changed in  
199 1995, and the new Campelen trawl is more effective at catching the smallest cod (Lilly et al.  
200 2003).

201 For 2J3KL cod, sample sizes of fish aged 7 years and older dropped to very low levels in  
202 the early 1990s (Lilly et al. 2003); robust estimates of the parameters describing growth and  
203 maturation at these ages could therefore not be obtained. Accordingly, analyses of maturation  
204 patterns were performed on 3-6 year old fish. Most males in 2J3KL are mature at age 7, and  
205 most females in 2J3KL are mature at age 8 (Lilly et al. 2003). For 3NO and 3Ps cod, analyses  
206 were performed on 3-8 year old fish. The statistical analyses were based on a total sample of  
207 57,532 fish (Table 1).

208 The spring data from Division 3L were included mainly for comparison with the autumn  
209 survey in this area. This comparison will determine if sampling fish in the fall, several months  
210 before spawning, has an impact on the results. The cod considered in this study spawn mainly  
211 during a 3-4 month period in late winter and spring (Hutchings and Myers 1993; Myers et al.  
212 1993), and it is possible that recruit spawners could develop gonads over the winter. Unless  
213 otherwise specified, “Division 3L” will hereafter refer to the autumn survey.

215    **Maturation reaction norms**

216       The probabilistic reaction norm for age and size at maturation is defined by the age- and  
217       size-specific probabilities with which an immature individual matures during a given time  
218       interval (Heino et al. 2002a). A description of the entire reaction norm involves specifying  
219       these probabilities for all relevant ages and sizes. For many purposes, it will be convenient to  
220       plot only the reaction norm midpoints, i.e., those combinations of age and size for which the  
221       estimated probability of maturing is 50%.

222       Maturation reaction norms should not be confused with other quantities, known as  
223       maturity ogives, traditionally used for describing a population's maturation status by  
224       estimating the proportion of mature individuals at a given age. The development of methods  
225       for estimating probabilistic maturation reaction norms was motivated by realizing that  
226       maturity ogives depend not only on the inherent maturation tendency of individuals (which is  
227       genetically coded) but also on the prevailing conditions for growth and survival (which affect  
228       the ogives both directly and through phenotypic plasticity). By contrast, the probabilistic  
229       reaction norm approach overcomes the potential confounding effects of growth and mortality,  
230       by estimating maturation probabilities conditional on individuals having reached a certain age  
231       and size. Variation in growth will thus only influence which parts of a reaction norm can be  
232       observed, but are expected to leave the position of the reaction norm unchanged. A consistent  
233       shift in the position of the reaction norm itself is thus strongly indicative of an evolutionary  
234       change in maturation (Stearns and Koella 1986; Heino et al. 2002a). This view assumes that  
235       maturation reaction norms are under genetic control and may evolve in response to selection  
236       pressures (Stearns and Koella 1986; Via and Lande 1985). There is evidence for genetic  
237       variation in reaction norms in fishes, both for early life-history traits (Haugen and Vøllestad  
238       2000) and for sexual maturation (McKenzie et al. 1983).

239 The data available for this study do not distinguish between first-time and repeat  
240 spawners. To estimate the probability of maturing, we used a refinement of the probabilistic  
241 reaction norm method (Barot et al. 2004a) by which the probability of maturing at age  $a$  and  
242 size  $s$ , denoted by  $m(a,s)$ , is derived from the probability of being mature at age  $a$  and size  $s$ ,  
243 denoted by  $o(a,s)$ , and from the mean annual growth increment at age  $a$ ,  $\Delta s(a)$ ,

244

245 (1) 
$$m(a,s) = [o(a,s) - o(a-1,s - \Delta s(a))] / [1 - o(a-1,s - \Delta s(a))],$$

246

247 where  $\Delta s(a)$  refers to the length gained from age  $a-1$  to age  $a$ . The function  $o(a,s)$  is referred  
248 to as the age- and size-based maturity ogive. The above equation for  $m(a,s)$  determines the  
249 probability of maturing as the frequency of fish that have matured (numerator) relative to the  
250 frequency of fish that could have matured (denominator). The equation is exact only when  
251 immature and mature individuals within a given age- and size-class have the same survival  
252 and growth rates. As demonstrated by Barot et al. (2004a), this estimation is relatively robust  
253 to a relaxation of this assumption.

254 Estimating maturation probabilities thus involves four steps: (1) estimation of maturity  
255 ogives, (2) estimation of growth rates, (3) estimation of the probabilities of maturing, and (4)  
256 estimation of confidence intervals around the obtained maturation probabilities. Maturity  
257 ogives were estimated by fitting logistic regression models to the data (Collett 2003), with  
258 individual maturity state (juvenile or mature) as a binary response variable. We carried out  
259 separate analyses for each sex and NAFO Division (Divisions 3N and 3O were pooled to  
260 accommodate for their small samples sizes). We were not able to analyze the full interaction  
261 between cohort, age, and body length, while using cohort and age as factors. Barot et al.  
262 (2004a) showed that such a full model requires sample sizes of about 100 individuals per  
263 cohort and age-class in order to obtain robust estimates. Therefore, our ogive model had to be

264 simplified. By inspecting parameter estimates and their errors, and through standard model  
265 selection (Collett 2003) based on different candidate models, we decided to model age as a  
266 variate (linear effect) while keeping cohort as a factor; also the interaction effect between  
267 cohort and age could be retained in the model,

268

269 (2)  $\text{logit}(o) = \beta_0 + \beta_1 \cdot \text{length} + \beta_{2,c} + \beta_3 \cdot \text{age} + \beta_{4,c} \cdot \text{age},$

270

271 where  $c$  denotes cohort. The cohort $\times$ age interaction (fifth term) is needed for detecting age-  
272 dependent temporal changes in the probability of being mature. Growth was estimated as the  
273 difference in mean body length between two consecutive ages of a cohort. Reaction norm  
274 midpoints were estimated by fitting logistic regression models to the reaction norm estimates,  
275  $m(a,s)$ , independently for each age and cohort,

276

277 (3)  $\text{logit}(m) = \beta_0 + \beta_1 \cdot \text{length},$

278

279 and substituting 0.5 for  $m$  (Barot et al. 2004a).

280 As described above, probabilities of maturing are obtained through a sequence of  
281 statistical analyses. Since confidence intervals for the reaction norm parameters thus cannot  
282 be obtained directly, bootstrap techniques are used instead (Manly 1997). A bootstrapped  
283 sample was constructed for each cohort and age, where individuals are chosen at random with  
284 replacement from the original data set. The resampling was repeated 1000 times. We fitted  
285 linear regression models to the reaction norm midpoints in order to test for temporal trends in  
286 maturation. Confidence intervals around the regression parameters were derived from the  
287 1000 bootstrap replicates, with the 2.5% and 97.5% percentiles being set as lower and upper  
288 confidence limits, respectively. All analyses were performed without weighting the

289 observations by population abundance at length (Morgan and Hoenig 1997; Barot et al.  
290 2004a), since preliminary analyses revealed that such weighting did not affect the conclusions  
291 about the data but tended to introduce more noise in the model estimates.

292

293 **Survival and age at 50% maturity**

294 Mainly for descriptive purposes, we present estimates of annual survival rates and of the  
295 traditional ogive-based measure of maturation, the age at 50% maturity. Annual survival  
296 probabilities  $S_{a,y}$  at age  $a$  in year  $y$  were estimated from survey catch data as

297

298 (4)  $S_{a,y} = C_{a,y}/C_{a,I,y,I},$

299

300 where  $C_{a,y}$  is the catch abundance per unit effort at age  $a$  in year  $y$  (Brattey et al. 2003; Lilly et  
301 al. 2003; Healey et al. 2003). The change in survey gear that took place in 1995 (Engel trawl  
302 replaced with Campelen trawl) could potentially have influenced trends in survival, hence the  
303 Engel data have been transformed to Campelen equivalents (for details, see Lilly et al. 2003).  
304 These Campelen equivalents were available for the years 1983-1994. Age at 50% maturity  
305 was estimated from logistic regression models with year as a factor and age as a variate,

306

307 (5)  $\text{logit}(o) = \beta_0 + \beta_1 \cdot \text{age} + \beta_{2,y} + \beta_{3,y} \cdot \text{age}.$

308

309 **Results**

310 **Survival, growth, and age at 50% maturity**

311 The estimates of annual survival probabilities are relatively noisy, but very low values are  
312 found in the early 1990s (Fig. 2). The estimates are generally higher again during the  
313 moratorium years (Fig. 2). Annual length increments, averaged for 4-6 year old cod, lie

314 between 4 and 12 cm per year (Fig. 3). The growth estimates are lower in the north (Division  
315 2J and 3K) compared to the south (Division 3NO and 3Ps, Fig. 3). There are no clear  
316 temporal trends in growth rates, but the lowest estimates are found in the early to mid-1990s  
317 (Fig. 3). In Divisions 2J, 3K, and 3L, the age at 50% maturity in females decreased from  
318 about 6 years in the 1980s to about 5 years in the mid-1990s (Fig. 4). In Divisions 3NO and  
319 3Ps, the age at 50% maturity in females varied between 5.5 and 7 years in the 1970s and  
320 1980s and decreased to about 4.5 to 5.5 years in the 1990s (Fig. 4). Male age at 50% maturity  
321 is about one year below female age at 50% maturity, and shows a similar trend over time (Fig.  
322 4). Our analyses agree with results that have been reported earlier in terms of instantaneous  
323 total mortalities, mean body length at age, and maturity ogives (Brattey et al. 2003; Healey et  
324 al. 2003; Lilly et al. 2003).

325

### 326 **Maturation reaction norms**

327 We were able to estimate maturation reaction norms for 2 to 3 ages for a given sex and  
328 Division. For younger or older fish outside such an age bracket, data were either too sparse or  
329 too skewed towards juvenile or mature individuals. As an example, we show the reaction  
330 norms for female and male cod of the 1980 cohort in Division 3Ps. These reaction norms had  
331 negative slopes, meaning that the body length at which the cod reach a given maturation  
332 probability decreases with age (Fig. 5). Furthermore, the male reaction norms were positioned  
333 below the female reaction norms (Fig. 5), implying that for a given age and body length, a  
334 male has a higher maturation probability than a female. These patterns were qualitatively  
335 similar for most other cohorts for which reaction norms could be estimated (additional  
336 reaction norms are not shown, but can be derived from Figs. 6 and 7).

337 Maturation patterns varied throughout the survey period. Most notably, there is a  
338 consistent temporal trend in all five geographic areas (2J, 3K, 3L, 3NO, and 3Ps) and for both

339 males and females: reaction norm midpoints (i.e., age-specific body lengths resulting in a  
340 50% probability of maturing) decline by about 15-25 cm through the 1980s and early 1990s  
341 (Figs. 6 and 7, Table 2). This decline in reaction norm midpoints means that maturation at a  
342 given growth rate shifted toward earlier ages and smaller body lengths. Furthermore, there  
343 appears to be a moment in time, around 1993-1995, from which onwards there is no further  
344 decrease in reaction norm midpoints (Figs. 6 and 7, Table 2). We used the year in which each  
345 moratorium was introduced as a logical break point for analyzing these finer patterns in the  
346 data. For the period subsequent to the start of each moratorium there is evidence for  
347 differences among the sexes in the trends in reaction norm midpoints. The females show a  
348 significantly positive slope in all geographic areas, although not always at age 6 years, due to  
349 sparse data at that age (Table 2). Males show a significantly positive slope only in the 3K and  
350 3L Divisions – and their slopes are generally not as steep as for the females in the same areas  
351 (Table 2).

352 Together, Figs. 5-7 suggest that (independent of differences in growth and survival) males  
353 tend to mature at smaller body sizes and younger ages compared to females, and that there is a  
354 spatial trend by which maturation probabilities increase with latitude for all ages and sizes.  
355 These patterns are best seen by comparing smoothed temporal trends in reaction norm  
356 midpoints at age 5 years for all Divisions (Fig. 8).

357 Notice that changes in the observed sizes and maturity frequencies at each age occurring  
358 over winter could, in principle, induce differences in reaction norm midpoints estimated from  
359 autumn vs. spring surveys. Reassuringly, for the 3L Division, for which we have data from  
360 both autumn and spring, this appears not to be the case: the estimated reaction norm  
361 midpoints are very similar (Fig. 9). Temporal overlap between the two surveys in 3L is  
362 reduced because, due to the scarcity of data, reaction norm midpoints could not be estimated  
363 from spring data from about 1990 onwards.

364 From a management perspective, the following question is of high relevance: at what  
365 moment in time could the decline in reaction norm midpoints have been detected? We have  
366 explored this question by going back in time (in steps of one year from the year in which the  
367 moratorium was introduced), computing reaction norm midpoints and slopes from the  
368 restricted data that was available to managers at that time. We limited this analysis to 6 year  
369 old females, as these exhibited relatively precise estimates for the period up to the  
370 moratorium. This retrospective analysis indicates that the negative slopes in reaction norm  
371 midpoints could have been detected in all areas by 1990. In some divisions, these trends could  
372 have been picked up even earlier: negative slopes could have been detected in the early 1980s  
373 in 3Ps; in the mid 1980s in 2J, 3K, and 3NO; and around 1990 in 3L (Fig. 10).

374

## 375 **Discussion**

376 This study provides evidence for contemporary life-history evolution in one of the world's  
377 leading food fish, the Atlantic cod. We show that the maturation schedule of Atlantic cod off  
378 southern Labrador and Newfoundland shifted towards earlier ages and smaller body sizes in  
379 the 1980s and early 1990s. This shift is demonstrated through changes in the reaction norm  
380 for age and size at maturation, and thus is not confounded by concomitant changes in growth  
381 or survival. The same trend was shown independently for both female and male cod from five  
382 neighbouring geographic areas (NAFO Divisions 2J, 3K, 3L, 3NO, and Subdivision 3Ps). Our  
383 findings strongly suggest that the collapse of the cod populations off southern Labrador and  
384 Newfoundland, which took place during the late 1980s and the early 1990s, was a distinct  
385 selective episode that favoured early-maturing genotypes relative to late-maturing genotypes.  
386 This conclusion is in agreement with earlier findings based on a subset of the data analyzed  
387 here (female northern 2J3KL cod; Olsen et al. 2004).

388 We note that age and size will typically not explain all variation in maturation, so that  
389 trends in the reaction norms could still be influenced by hypothetical trends in phenotypically  
390 plastic responses that are unrelated to growth, age, or size. First, a cod in good condition will  
391 likely have a higher probability of maturing than a similarly sized and aged cod in poor  
392 condition (Marteinsdottir and Begg 2002). Cod off southern Labrador and eastern  
393 Newfoundland (NAFO Divisions 2J3KL) experienced a decrease in body condition during the  
394 period of collapse, except for fish in parts of the 3L Division (Bishop and Baird 1994; Krohn  
395 et al. 1997). The net effect of this would be to *delay* maturation, contrary to observations. It is  
396 not likely, therefore, that trends in body condition have caused the trends in reaction norms  
397 reported here for these areas. Second, the estimated reaction norms could be influenced by the  
398 social environment experienced by the fish. For example, in the platyfish (*Xiphophorus*  
399 *maculatus*), the presence of dominant males has been shown to suppress maturation of  
400 subordinate males (Sohn 1977). It seems unlikely, though, that the intensity of such a social  
401 effect should increase while population density was exhibiting catastrophic decline. Third,  
402 there could be a residual effect of temperature on the maturation reaction norms. For North  
403 Sea plaice (*Pleuronectes platessa*) it has been shown that the probability of maturing at a  
404 given age and length increased significantly with increased temperature 2 and 3 years prior to  
405 maturation (Grift et al. 2003). However, the collapse of the cod populations off Labrador and  
406 Newfoundland coincided with a prolonged period of low water temperatures (Drinkwater  
407 2002). The net effect of this – as suggested by the study of North Sea plaice – would be to  
408 displace the reaction norms toward *older* ages and *larger* sizes, while the opposite was in fact  
409 observed.

410 We also wish to highlight a semantic issue that sometimes leads to confusion. The term  
411 maturation “reaction norm” implies, through its historical usage in the literature, that the  
412 variation of age and size at maturation along the reaction norm is mostly a phenotypically

413 plastic response, in this case to variation in growth. Our usage of this term thus implies that  
414 variation *along* the reaction norm is mostly caused by environmental, as opposed to genetic,  
415 factors. While it is known that genetic variability in growth exists, and that growth rates may  
416 thus evolve as a response to selective harvesting (Conover and Munch 2002; see also Sinclair  
417 et al. 2002, Munch et al. this issue), it is very unlikely that growth variation in a species  
418 exposed to an environment as unpredictable as that of Atlantic cod is primarily genetic. Even  
419 if this were different (perhaps for another species), the valuable descriptive properties of these  
420 reaction norms do not depend on their naming, and thus not on the actual origin of growth  
421 variation. In the longer run, future research may aim to determine whether – and, if so, how –  
422 maturation evolution and growth evolution are interacting, both ecologically and genetically.

423 We found that the age-specific body length at which maturation probability reaches 50%,  
424 referred to as the reaction norm midpoint in this study, was smaller for male cod as compared  
425 to female cod. This implies that, for a given growth rate, male cod will tend to mature at  
426 earlier ages and smaller body sizes. This sex difference in maturation pattern conforms well to  
427 results based on the more traditional method of maturity ogives (Brattey et al. 2003; Morgan  
428 2000), considering that there seems to be no major sex difference in growth (Fig. 3). Also the  
429 fact that females show a more pronounced reversal of maturation patterns during the  
430 moratorium years supports the suggestion that selection pressures have differed, and continue  
431 to differ, between the sexes. For female cod, a large body size offers an indisputable fitness  
432 advantage, in terms of both increased fecundity and improved offspring quality (Trippel  
433 1998). For male cod, on the other hand, the benefits of large body size are less obvious. Tank  
434 experiments in which female cod had access to both small and large males revealed no  
435 positive association between male body size and reproductive success; in fact, many of the  
436 smaller males exhibited a higher success than their larger-sized competitors (Rakitin et al.  
437 2001).

438 Our data indicate that from about 1993-1995, after the closing of the fisheries, the trends  
439 in the maturation norms are halted and, for females, even show signs of reversal. To some  
440 extent, the signs of reversal are a surprising result, because, in theory genetic change caused  
441 by fishing will not be easily reversed: selection for early maturation appears to be much  
442 easier, and faster, than for late maturation (Law and Grey 1989). Still, field-experiments on  
443 freshwater fish have documented rapid evolution towards delayed maturation when predation  
444 pressure was relaxed (Reznick et al. 1990). It is possible that the fitness benefits of large size  
445 in female cod (as discussed above) are stronger than until now considered in models. Also, it  
446 is possible, in theory, that immigration of genotypes with different maturation schedules could  
447 have influenced the recent trends in maturation reaction norms. Importantly, the period since  
448 initiation of the moratoria has been only a decade; to better understand whether the  
449 conjectured trend in maturation schedules is borne out we shall have to await the results of  
450 future research surveys.

451 We also found evidence for a geographical trend by which the age-specific body length at  
452 50% maturation probability decreased with increasing latitude (see also Morgan et al. 1994).  
453 This north-south gradient was substantial, and opposite to the effect of the latitudinal gradient  
454 in growth on the timing of maturation. We therefore suggest that our results reveal  
455 countergradient variation in maturation tendency (Conover and Schultz 1995): the capacity  
456 for early maturation (as determined by the cod's genetics) appears to be greatest in areas with  
457 the least opportunity for early maturation (as determined by the phenotypically plastic  
458 consequences of differential growth). For instance, in the early 1980s, the reaction norm  
459 midpoints of 6 year old females from off southern Newfoundland (Subdivision 3Ps) were  
460 around 70 cm, as compared to only 50 cm for females from off southern Labrador. This  
461 finding suggests that genetic differences, consistent with the selective pressures of local  
462 adaptation, exist in the maturation schedules of cod from different parts of the Labrador-

463 Newfoundland region. Tagging studies and population genetic studies corroborate that local  
464 population structure exists within this region (Templeman 1966; Ruzzante et al. 1998;  
465 Beacham et al. 2002). It thus seems likely that locally adapted life histories in Atlantic cod  
466 can evolve, despite the fact that cod is a highly mobile species inhabiting a marine  
467 environment without any obvious barriers to dispersal. As pointed out by Berkeley et al.  
468 (2004b) and Hutchings (2004), managers should thus take into account that marine exploited  
469 species may have a complex spatial population structure and life-histories that are evolving on  
470 a contemporary time scale.

471 Maturation reaction norms have also been estimated for other heavily exploited  
472 populations of Atlantic cod, from Georges Bank as well as the Gulf of Maine (Barot et al.  
473 2004b) in the northwest, and from the Norwegian Sea as well as the Barents Sea (Heino et al.  
474 2002a,b,c) in the northeast. Similar findings have been obtained for North Sea plaice (*P.*  
475 *platessa*, Grift et al. 2003; see also Rijsdorp 1993) and American plaice (*Hippoglossoides*  
476 *platessoides*, Barot et al. in press). These studies provide evidence for adaptive changes in  
477 maturation schedules that point in the very same direction as those documented in this study  
478 of Labrador and Newfoundland cod.

479 We suggest that monitoring maturation reaction norms for age and size at maturation may  
480 aid decision making in the management of exploited marine resources in general, and of  
481 Atlantic cod in the Newfoundland-Labrador region in particular. First, estimates of age- and  
482 length-specific maturation probabilities are needed to parameterize age- and length-structured  
483 population models (Frøysa et al. 2002), and hence provide important input for a broad  
484 spectrum of population assessment purposes. Second, information on trends in the maturation  
485 process may serve as a helpful warning signal with regard to changes in population size and  
486 recruitment potential. With the collapse of the cod populations off Labrador and  
487 Newfoundland in mind, Hutchings and Myers (1995) argued that the sustainability of any

488 fishery clearly depends on quantifying a wide range of biological indicators of population  
489 health. Specifically, Trippel (1995) suggested that the age  $A_{50}$  at which 50% of fish are mature  
490 holds promise as one such “stress” indicator. We build on this argument and put forward  
491 maturation reaction norms as a biological indicator with important advantages over  $A_{50}$ . A  
492 reduction in  $A_{50}$  is ambiguous in that it may reflect either fisheries-induced selection  
493 favouring early maturation, or maturation facilitated by faster individual growth in response  
494 to declining stock size. Both of these possibilities imply that fishing heavily impacts the  
495 population, which hence may be considered as being “stressed”. However,  $A_{50}$  may also  
496 decline if maturation is merely facilitated by a temperature increase or when the survival of  
497 mature fish increases. Neither of these scenarios represents a cause of concern for the  
498 management of a stock. By contrast, estimation of maturation reaction norms reveals changes  
499 in the maturation tendency itself, as shown here for the cod populations off Labrador and  
500 Newfoundland in the 1980s. A more robust indicator of population health may therefore be  
501 the length  $L_{P50}$  (Grift et al. 2003) at which the probability of maturing reaches 50% for a given  
502 age. The methodology described and utilized here enables estimation of  $L_{P50}$ .

503 In summary, this study shows that maturation of Labrador and Newfoundland cod shifted  
504 towards earlier ages and smaller body sizes during the severe collapse of these populations in  
505 the late 1980s and early 1990s. The use of reaction-norm methodology removes confounding  
506 effects of growth or survival, and thus provides stronger evidence for changes in the  
507 underlying maturation process than previous analyses could.

508

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709 **Table 1.** Sample sizes for surveys of Atlantic cod (*Gadus morhua*) conducted annually by  
710 the Canadian Department of Fisheries and Oceans in North Atlantic Fishery Organization  
711 (NAFO) Divisions 2J, 3K, 3L, 3NO, and Subdivision 3Ps.

Division	Survey	Years	Ages	Females	Males	Total
2J	Autumn	1977-2002	3-6	3711	3773	7484
3K	Autumn	1977-2002	3-6	4667	4364	9031
3L	Autumn	1981-2002	3-6	3133	3131	6264
3L	Spring	1971-2002	3-6	4077	3962	8039
3NO	Spring	1971-2002	3-8	6822	6764	13586
3Ps	Spring	1972-2002	3-8	6958	6170	13128
Total				29368	28164	57532

712 No data exist for spring 1974 in Subdivision 3Ps, spring 1983 in 3NO, and autumn 1984 in  
713 3L.

714 **Table 2.** Temporal trends in maturation reaction norm midpoints in Atlantic cod from  
 715 NAFO Divisions 2J, 3K, 3L, 3NO, and Subdivision 3Ps. Regressions are shown for pre-  
 716 moratorium years (including the year in which each moratorium was declared), as well as for  
 717 subsequent years. The moratorium was initiated in July 1992 in Divisions 2J, 3K, and 3L; in  
 718 February 1994 in Divisions 3NO; and in August 1993 in Subvision 3Ps. The moratorium was  
 719 lifted in 1997 in 3Ps; this is not taken into account in the analyses.

Regression slope, cm·y <sup>-1</sup> (95% C.I.)				
Division	Sex	Age, y	Pre-moratorium	Moratorium
2J	F	5	-1.15 (-2.19, -0.87)	1.06 (0.68, 2.33)
2J	F	6	-0.67 (-0.99, -0.37)	*
3K	F	5	-0.82 (-1.88, -0.50)	0.51 (0.26, 0.79)
3K	F	6	-0.97 (-1.23, -0.75)	1.00 (-0.24, 2.29)
3L	F	5	-0.84 (-3.36, 0.88)	0.63 (0.25, 1.03)
3L	F	6	-0.39 (-1.04, 0.07)	0.98 (0.16, 2.74)
3NO	F	5	-0.71 (-1.18, -0.56)	1.69 (0.63, 2.66)
3NO	F	6	-0.55 (-1.15, -0.40)	0.99 (-3.89, 11.55)
3Ps	F	5	-1.05 (-1.33, -0.78)	0.90 (0.19, 1.89)
3Ps	F	6	-1.34 (-1.68, -1.01)	1.25 (-0.84, 3.00)
2J	M	4	-0.80 (-1.20, -0.62)	0.25 (-0.50, 0.72)
2J	M	5	-0.82 (-1.07, -0.69)	*
3K	M	4	-0.61 (-1.08, -0.43)	0.30 (0.057, 0.53)
3K	M	5	-0.49 (-0.73, -0.33)	-0.17 (-1.63, 1.07)
3L	M	4	-0.69 (-1.16, -0.12)	0.33 (0.04, 0.62)

3L	M	5	-0.60 (-1.19, -0.47)	1.02 (0.39, 2.13)
3NO	M	4	-0.38 (-0.70, -0.053)	-1.83 (-10.78, 0.23)
3NO	M	5	-0.65 (-1.31, -0.52)	0.43 (-3.12, 1.92)
3Ps	M	4	-0.70 (-0.96, -0.46)	-0.63 (-1.69, 0.36)
3Ps	M	5	-0.99 (-1.23, -0.81)	-1.24 (-4.57, 0.63)

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720 \*Not estimable due to sparse data.

721 **Fig. 1.** Study area, showing physiographic features and Northwest Atlantic Fisheries  
722 Organization (NAFO) Divisions 2J, 3K, 3L, 3NO, and Subdivision 3Ps.

723

724 **Fig. 2.** Mean annual survival rates of 4-6 year old Atlantic cod from NAFO Divisions 2J,  
725 3K, 3L, 3NO, and Subdivision 3Ps, fitted with a locally weighted regression smoother. The  
726 smoothing parameter (span) is set to 0.5. Point estimates exceeding 1 are not shown but were  
727 included when fitting the regression.

728

729 **Fig. 3.** Mean annual length increments of 4-6 year old Atlantic cod from NAFO Divisions  
730 2J, 3K, 3L, 3NO, and Subdivision 3Ps, fitted with a locally weighted regression smoother.  
731 The smoothing parameter (span) is set to 0.5.

732

733 **Fig. 4.** Ages at 50% maturity of Atlantic cod from NAFO Divisions 2J, 3K, 3L, 3NO, and  
734 Subdivision 3Ps, fitted with a locally weighted regression smoother. The smoothing  
735 parameter (span) is set to 0.3.

736

737 **Fig. 5.** Maturation reaction norms of Atlantic cod of the 1980 cohort from NAFO  
738 Subdivision 3Ps, shown in terms of body lengths at which the probability of maturing equals  
739 25%, 50% (reaction norm midpoint), and 75% (black continuous lines). Growth rates are  
740 depicted as arithmetic mean length at age (grey continuous lines) together with 5% and 95%  
741 percentiles (grey dotted lines).

742

743 **Fig. 6.** Temporal trends in maturation reaction norm midpoints of female Atlantic cod at  
744 ages 5 and 6 years, from NAFO Divisions 2J, 3K, 3L, 3NO, and Subdivision 3Ps. Some  
745 cohorts are missing owing to insufficient data.

746

747 **Fig. 7.** Temporal trends in maturation reaction norm midpoints of male Atlantic cod at ages  
748 4 and 5 years, from NAFO Divisions 2J, 3K, 3L, 3NO, and Subdivision 3Ps. Some cohorts  
749 are missing owing to insufficient data.

750

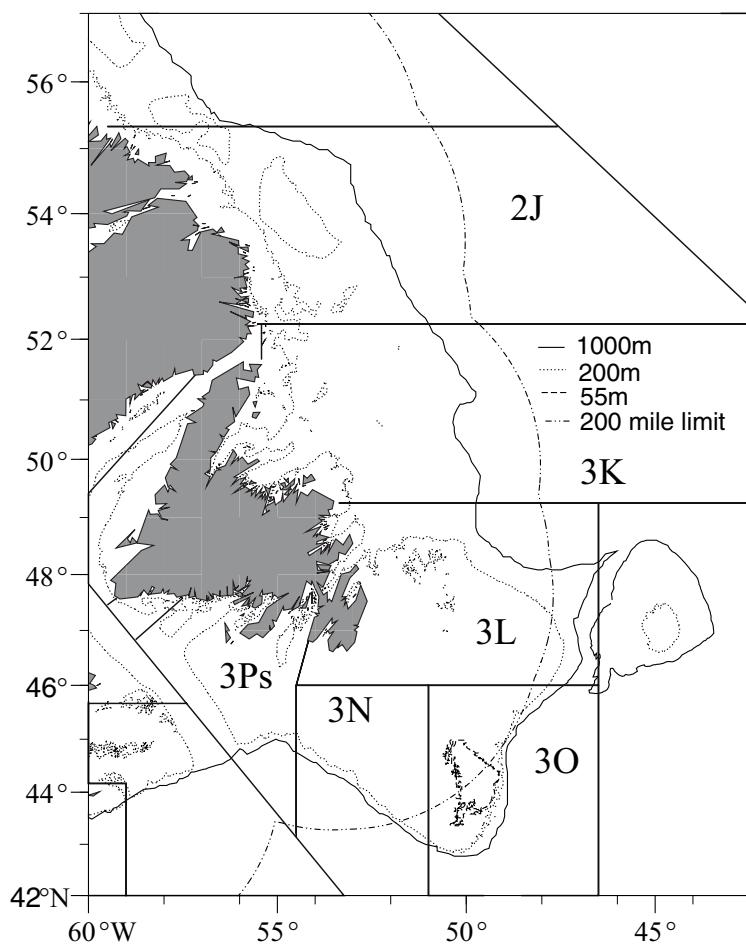
751 **Fig. 8.** Maturation reaction norm midpoints at age 5 years for Atlantic cod from NAFO  
752 Division 2J (dashed black line), 3K (dotted black line), 3L (continuous black line), 3NO  
753 (continuous grey line), and Subdivision 3Ps (dashed grey line); fitted with a locally weighted  
754 regression smoother. The smoothing parameter (span) is set to 0.4. The arrows indicate how  
755 the maturation reaction norms are ordered with respect to increasing latitude (see also Fig. 1).

756

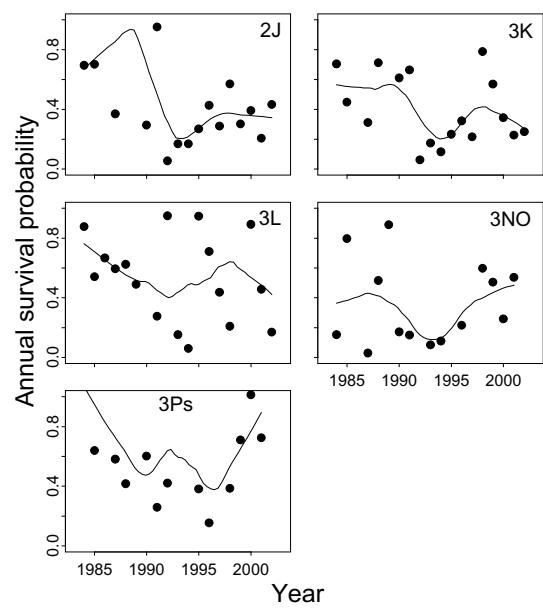
757 **Fig. 9.** Maturation reaction norm midpoints for females at age 6 years and males at age 5  
758 years of Atlantic cod from NAFO Division 3L, based on spring survey data (dashed line) and  
759 autumn survey data (continuous line), respectively, fitted with a locally weighted regression  
760 smoother. The smoothing parameter (span) was set to 0.4.

761

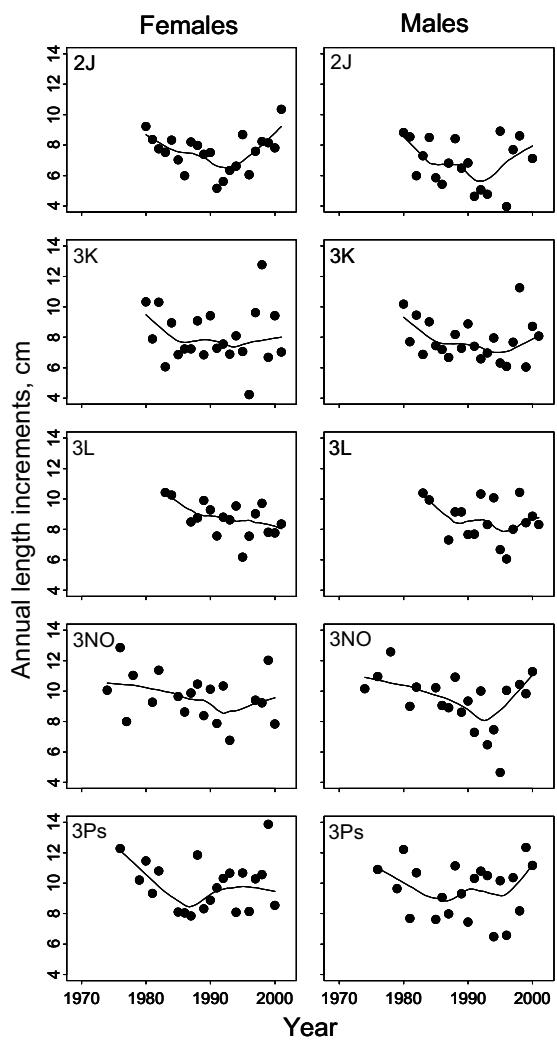
762 **Fig. 10.** Probability of a negative trend in reaction norm midpoints, estimated for 6 year old  
763 female Atlantic cod when analysis is retrospectively restricted to only part of the available  
764 time series, up to and including the given terminal year. The last terminal year shown  
765 corresponds to the year in which the moratorium was initiated. Dotted lines show, for  
766 reference, the 80% level of the probability of a negative trend. The probabilities were  
767 calculated as the proportion of 1000 bootstrap replicates yielding a negative slope.



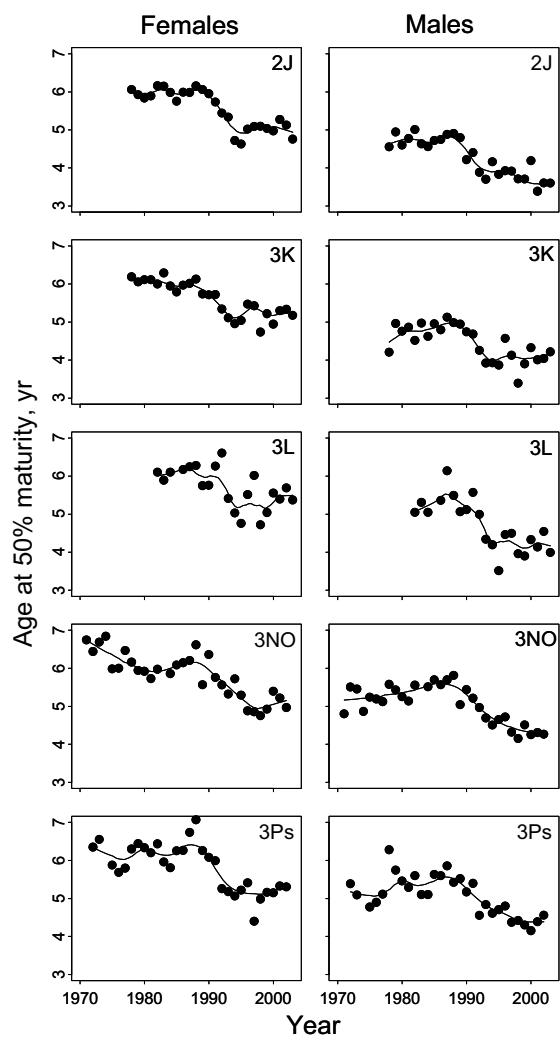
**Figure 1**



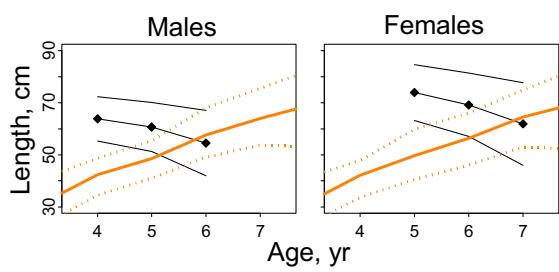
**Figure 2**



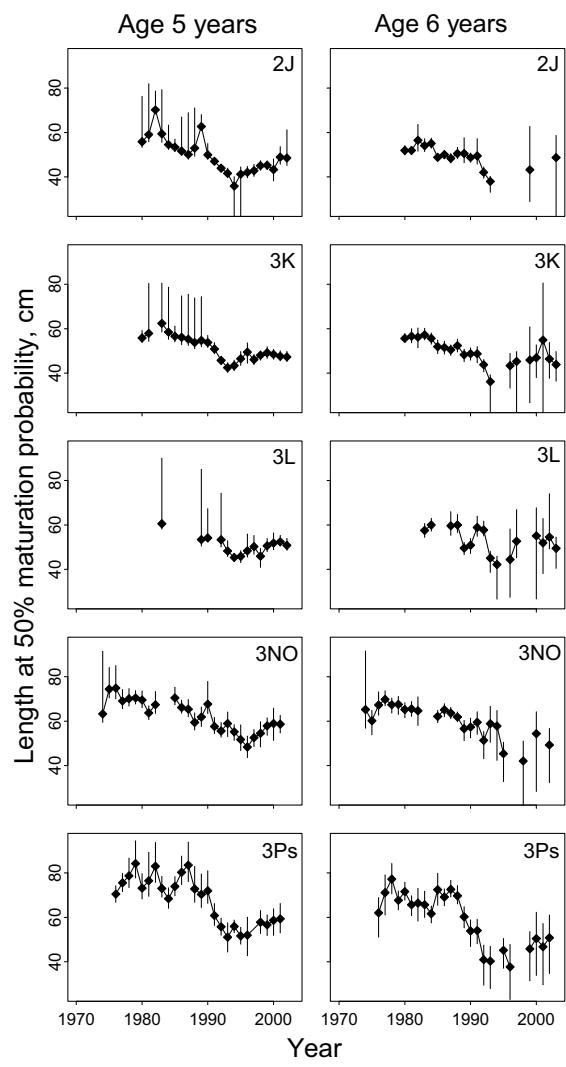
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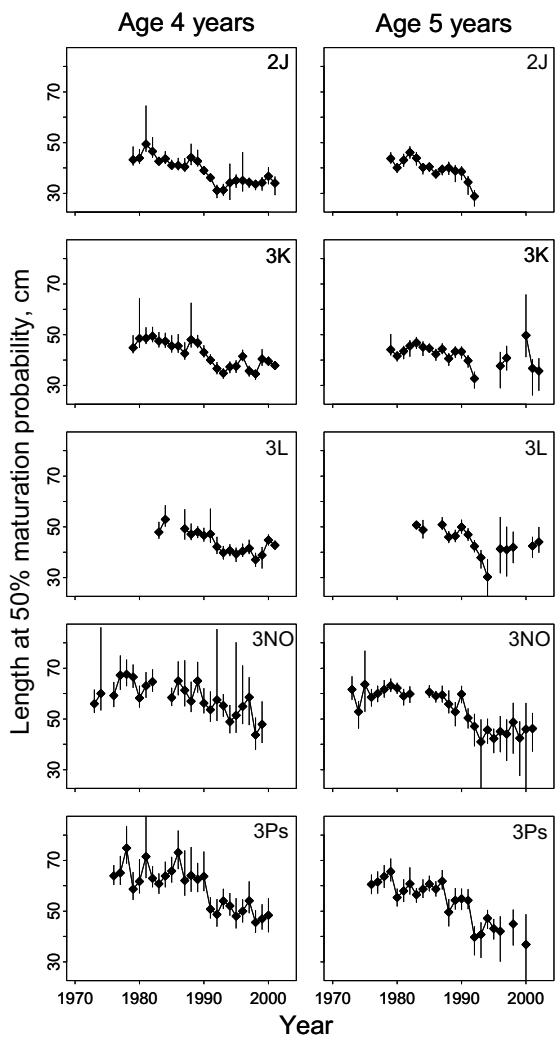
**Figure 4**



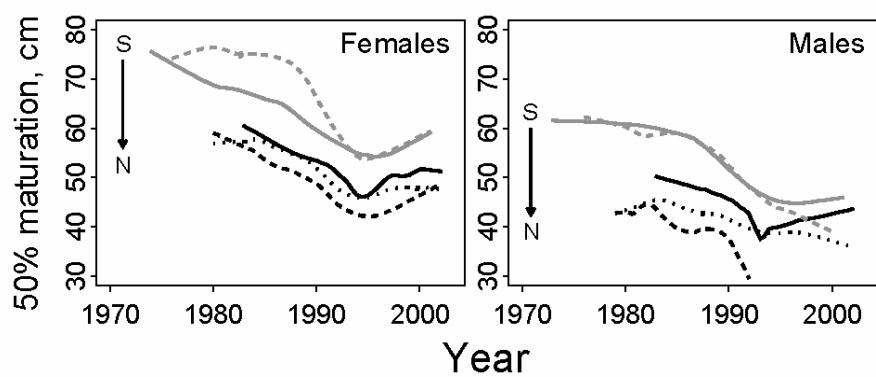
**Figure 5**



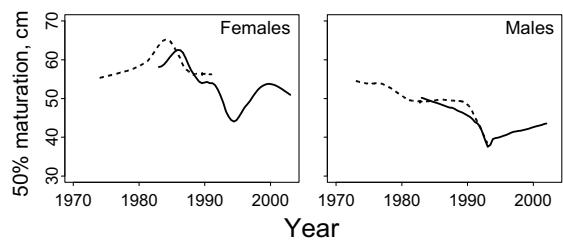
**Figure 6**



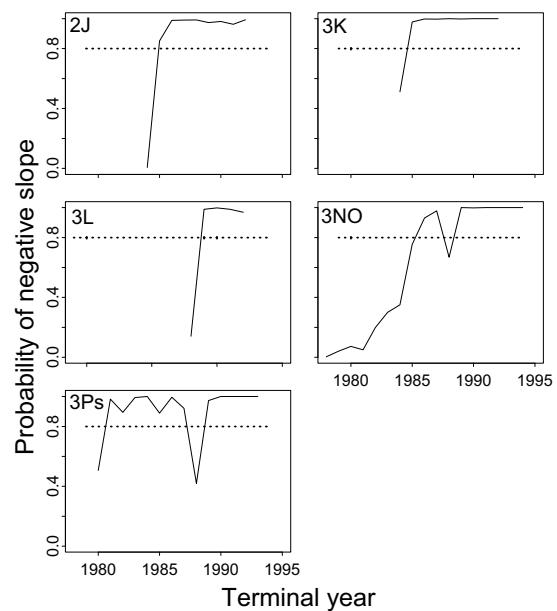
**Figure 7**



**Figure 8**



**Figure 9**



**Figure 10**