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## Interim Report

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### State-dependent Energy Allocation in Cod (*Gadus Morhua*)

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1 **State-dependent energy allocation in cod (*Gadus morhua*)**

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## 7 **Abstract**

8 Growth and maturation are processes that are tuned to the external environment an  
9 individual is likely to experience, where food availability, the mortality regime, and events  
10 necessary to complete the life cycle are of special importance. Understanding what influences  
11 life history strategies and how changes in life history in turn influence population dynamics  
12 and ecological interactions are crucial to our understanding of marine ecology and  
13 contemporary anthropogenic induced change. We present a state-dependent model that  
14 optimises life-long energy allocation in iteroparous fish. Energy can be allocated to growth or  
15 reproduction, and depends in the individual's age, body length, stored energy, and the state of  
16 the environment. Allocation and the physiological processes of growth, storing energy, and  
17 reproduction are modelled mechanistically. The model is parameterised for Atlantic cod  
18 (*Gadus morhua*); more specifically for the Northeast Arctic cod stock. Growth and maturation  
19 predicted by the model fit well with field observations, and based on a further investigation of  
20 cod reproduction in the model we conclude that the model has the ability to recapture  
21 complex life history phenomena, e.g. indeterminate growth and skipped spawning, and  
22 therefore provides an important tool that can improve our understanding of life history  
23 strategies in fish.

24 **Keywords:** Life history evolution, energy allocation, state dependence, dynamic  
25 programming, *Gadus morhua*.

## 26 **Introduction**

27 Energy use may be divided into three broad categories – survival, growth, and  
28 reproduction. These interests are often conflicting as they are crucial for fitness in different  
29 ways. When is an individual predicted to grow to increase future reproduction, and when to  
30 reproduce? A large size often means a high reproductive success, but also a low probability of  
31 survival until reproduction can finally take place. When is growth predicted to be determinate,  
32 and when indeterminate? When is survival probability predicted to influence the optimal adult  
33 size? And in the balance between foraging rate and predation risk; when is an individual  
34 predicted to hide and when to feed (Krebs and Davies 1993)?

35 For an individual, energy is limited, and these questions represent multiple trade-offs in  
36 several dimensions that may be at work simultaneously. Energy allocation – how available  
37 energy is diverted towards alternative uses – is the mechanism that integrates the trade-offs  
38 through shaping the individual's growth trajectory. This trade-off is the essential core of life  
39 history theory (Fisher 1930).

40 Fisheries management is moving towards an ecosystem approach because ecological  
41 complexity confounds single-species management. At the same time, human-induced  
42 contemporary evolution is identified as the driving force behind observed changes in many  
43 marine ecosystems (Stokes and Law 2000; Conover and Munch 2002; Olsen et al. 2004).  
44 Because life history theory is an obvious link between ecology and evolution, it provides a  
45 tool to predict growth, maturation, and behaviour as ecological forcing changes. Alterations in  
46 allocation strategies propagate from individual characteristics via population structure to  
47 ecological interactions within and between species. This implies that life history theory  
48 should be highly relevant for fisheries science, and understanding the logic of life history  
49 theory an integral part of ecosystem management.



50 Consider as an example stock–recruitment relationships. Allocation to reproduction earlier  
51 or later in life is likely to influence the entire demographic structure and population dynamics.  
52 Both mature biomass and the stock’s overall egg production will be affected, through changes  
53 in maturity-, size-, and fecundity-at-age. Life history theory is, as such, the mechanistic basis  
54 for stock-recruitment relationships, and therefore central not only in disentangling stock-  
55 recruitment relationships today, but also when making predictions in light of fisheries-induced  
56 evolution or climate change.

57 Intuitively, an old individual should perhaps spend its energy differently from a young one,  
58 and being large at a given age harbours different opportunities than being small. Age and  
59 body length are likely to influence allocation and should therefore be included as states, i.e.  
60 information the individual has about itself and that may influence energy allocation (Houston  
61 and McNamara 1999; Clark and Mangel 2000). It is common knowledge that individual  
62 condition plays a central role both for growth and reproduction in various fishes (Kjesbu et al.  
63 1991; Burton et al. 1997; Lambert and Dutil 2000). Most organisms in fluctuating  
64 environments rely on stores to balance periods when energy is plentiful with periods of  
65 energy shortage. Fish and other animals often use lipid stores, either integrated in the muscle  
66 tissue (for example clupeids) or in the liver (typical for gadoids). Atlantic cod (*Gadus*  
67 *morhua*) belongs to the latter category, and the lipid-rich liver constitutes up to 9% of the  
68 body mass among mature fish (Yaragina and Marshall 2000). There is a close relationship  
69 between stored energy in the liver and fecundity, and total liver energy in a cod population  
70 has been shown to be a good proxy for total egg production (Marshall et al. 1999). Thus  
71 individual condition, interpreted as the amount of stored energy, directly affects reproductive  
72 success and survival.

73 Earlier life-history models investigating energy allocation in fish have used a fixed rule to  
74 describe lifelong allocation patterns: all available energy was allocated to growth up to a

75 variable age at sexual maturation, and a fixed proportion of the energy was diverted to  
76 reproduction from then on to maximise reproductive value (Roff 1983; Law and Grey 1989;  
77 but see also Strand et al. 2002). These models have provided great insight into life history  
78 strategies and the evolutionary dynamics of harvested fish stocks, but time is now ripe to  
79 extend the analyses. Here, we investigate state-dependent energy allocation in a  
80 physiologically realistic model based on the Atlantic cod. Using four discretised state  
81 variables (age, length, stored energy, and food availability), our model allows for  
82 approximately 6.4 million independent values to describe a four-dimensional allocation  
83 hypersurface. In the strict sense, this is also a fixed rule, but the rule is so complex that it  
84 specifies what to do in nearly all situations an individual can encounter throughout life.

85 Our aim is to formulate a flexible life history modelling tool. The high resolution enables  
86 seasonal patterns, as well as optimal size-, age-, and condition-dependent life history  
87 strategies to emerge, and introduces great flexibility with a sound biological basis into models  
88 of fish growth. The model makes very few life-history assumptions, while letting optimisation  
89 tools exhibit the best patterns of growth and reproduction. This would also be the growth  
90 trajectories supposedly favoured by natural selection, assuming no constraints. We show that  
91 the model fits well with field data and experimental work, and that it recaptures much of the  
92 ecological dynamics of the Northeast Arctic cod stock. In a companion paper, we apply the  
93 same model to analyse skipped spawning behaviour of cod (Jørgensen et al. this issue).

## 94 **Model description**

### 95 *Purpose*

96 We develop a state-dependent model that mechanistically describes energy allocation to  
97 growth and reproduction in fish. Since energy is a restricted resource, the life-long pattern in  
98 this allocation embodies many of the trade-offs that shape life history. The focus on energy  
99 allocation therefore fulfils the purpose of this model, which is to find the optimal life-history

100 under varying external forcing (e.g., fishing mortality, migration, and food availability).  
101 Throughout, we model the energy allocation processes as mechanistically correct as feasible,  
102 while retaining flexibility in how allocation can change with time and state. In this way we  
103 can use dynamic programming algorithms to find the optimal allocation pattern under the  
104 constraints given by the realistic and detailed description of physiology and ecology.

#### 105 *Structure*

106 The modelling approach in this paper uses dynamic programming to find optimal  
107 allocation strategies (Houston and McNamara 1999; Clark and Mangel 2000). The result is a  
108 state-dependent energy allocation rule that is a life history strategy. Thereafter, we run  
109 population simulations of many individuals following the life history strategy. During these  
110 population simulations, age and size distributions emerge and we can assess the implications  
111 of the life history strategy on growth, maturation, reproduction etc. The model is  
112 parameterised for the Northeast Arctic cod stock, which is a long-lived species with  
113 iteroparous reproduction. From their feeding grounds in the Barents Sea, the spawners  
114 migrate in spring to the Lofoten area where spawning takes place. The remainder of the year  
115 is used for growth and to rebuild energy stores. The time resolution of the model is months  
116 (discrete steps), and each month net energy intake is allocated between growth (to increase  
117 body size) and reproduction (building energy stores and later gonads). The optimal allocation  
118 is found by dynamic programming and depends on four states: age (in months, thus including  
119 season); body length (cm); size of energy stores (relative scale); and current feeding  
120 conditions. In the model, we consider only female cod.

#### 121 *Processes*

122 Energy allocated to growth irreversibly increases body length, while stored energy can be  
123 used for spawning (migration and egg production) or for metabolism during times when  
124 feeding conditions are poor (Fig. 1). Density-dependence is not included in the model.

Figure 1

125        *Concepts*

126        Optimal energy allocation is determined for each state combination with expected  
127        reproductive value as fitness measure. The result is a highly flexible multi-dimensional  
128        hypersurface that defines a life-history strategy, described by 6.4 million independent points  
129        (each point corresponding to a particular combination of the four states). Because rewarding  
130        analyses are virtually impossible on such amounts of data directly, we simulated populations  
131        of fish realising such life-history allocation strategies to let age-, size-, and condition-  
132        dependent patterns emerge at the individual and population level. A series of monthly energy  
133        allocations results in e.g. a time-series of growth, an age at sexual maturation, reproductive  
134        episodes with specific fecundities, and skipped spawning seasons (analysed separately in  
135        Jørgensen et al. this issue). There is no interaction between individuals in the simulated  
136        population, and individuals only have information about the four individual states. Food  
137        availability is auto-correlated in time to allow for more extended periods of  
138        advantageous/unfavourable environment. In the forward population simulation, this is  
139        modelled as a stochastic process. Since optimal strategies may use the predictive power of an  
140        auto-correlated environment to fine-tune allocation strategies (e.g., that a favourable  
141        environment is likely to persist for some time), current food availability was included as an  
142        extra state.

143        *Initialisation*

144        Juvenile fish were introduced in the model at age 2 years and body length 25 cm.  
145        Maximum age was set to 25 years, and the model was solved for body lengths up to 250 cm to  
146        avoid artificial boundary effects.

147        *Input*

148        Growth and maturation data from the literature were used to test parameter values and  
149        general properties.

150 *Submodels*

151 Details of the relationships defining the model are given below, followed by specific  
152 parameter values chosen to represent the Northeast Arctic cod stock.

153 **Individual physiology**

154 Body mass is divided into two compartments: soma and energy stores. Soma  $W_{\text{soma}}(L)$  (g  
155 wet weight) includes systematic structures such as skeleton, internal organs, the neural  
156 system, a minimum amount of muscle mass, and for which growth is irreversible. Additional  
157 energy may be stored above this level for reproduction or to enhance survival during periods  
158 of food shortage. Because weight usually increases with length with an exponent slightly  
159 above 3, the length-specific somatic weight (with no energy stores) can be written as function  
160 of  $W \propto L^{3+\varepsilon}$  where  $\varepsilon$  for many species falls between 0.1 and 0.4 (Ware 1978):

161 (Eq. 1) 
$$W_{\text{soma}}(L) = \frac{K_{\text{min}} \cdot L^{3+\varepsilon}}{100 \cdot L_{\text{std}}^{\varepsilon}},$$

162 where  $K_{\text{min}}$  is the minimum Fulton's condition factor  $K = W \cdot 100 \cdot L^{-3}$ , where weight is  
163 measured in g wet weight and length in cm (the resulting number varies around 1.0 and  
164 describes the fatness or body condition of an individual). For a given length,  $K_{\text{min}}$  represents  
165 the minimum body mass required for structures; death by starvation can be incorporated to  
166 occur at  $K_{\text{min}}$  or with increasing probability as  $K_{\text{min}}$  is approached. Similarly, there is a limit  
167 for how spherical the shape of an individual can be, and  $K_{\text{max}}$  is the maximum Fulton's  
168 condition factor that includes  $W_{\text{soma}}$  and full energy stores. This maximum reflects the  
169 physical limitations imposed by anatomy and the need to maintain other body functions while  
170 carrying stores, and in this model stores cannot be increased above the level set by  $K_{\text{max}}$ . For  
171  $\varepsilon \neq 0$ ,  $K_{\text{min}}$  and  $K_{\text{max}}$  must be specified for a given length  $L_{\text{std}}$  (cm).

172 Energy is normally stored partly as proteins by increasing muscle mass, and partly as lipids  
 173 either embedded in the muscles (common for salmonids) or stored separately in the liver  
 174 (typical for gadoids). The average energy density of these energy stores combined,  $\rho_E$  ( $J \cdot g^{-1}$ ),  
 175 has to be known. We assume that this density is constant, meaning that muscle proteins and  
 176 lipids are stored at a constant ratio above the minimum muscle mass included in  $W_{soma}$ . When  
 177 the amount of stored energy  $E$  (J) is known, total body mass  $W$  (g wet weight) can be  
 178 calculated as:

179 (Eq. 2a) 
$$W(L, E) = W_{soma}(L) + \frac{E}{\rho_E} ,$$

180 where  $E$  has to be less than or equal to the maximum energy that can be stored,  $E_{max}$  (J):

181 (Eq. 2b) 
$$E_{max}(L) = (K_{max} - K_{min}) \cdot \frac{\rho_E \cdot L^{3+\varepsilon}}{100 \cdot L_{std}^\varepsilon} .$$

182 Energy expenditure is calculated according to the bioenergetics model by Hewett and  
 183 Johnson (1992). Metabolic rate ( $MR$ ;  $J \cdot t^{-1}$ ) is the product of the standard metabolic rate ( $SMR$ ;  
 184  $J \cdot t^{-1}$ ) and an activity parameter  $Act_{Std}$  to include a routine level of activity:

185 (Eq. 3) 
$$MR = SMR \cdot Act_{Std} = \kappa_1 \cdot W(L, E)^{\beta_1} \cdot Act_{Std} , \quad Act_{Std} > 1 .$$

186 Here,  $\kappa_1$  ( $J \cdot g^{-\beta_1} \cdot t^{-1}$ ) is the coefficient and  $\beta_1$  mass exponent of the allometric function.

187 **Environment**

188 Food intake  $\phi$  ( $J \cdot t^{-1}$ ) is determined by food availability in the environment and a measure of  
 189 body size (body mass  $W$  (g) or body length  $L$  (cm)). A stochastic function  $\chi$  and seasonal

190 cycles  $C(t)$  can be incorporated to account for environmental variability in food availability.

191 Feeding intake would thus be

192 (Eq. 4a)  $\phi(W) = \chi \cdot C(t) \cdot \kappa_2 \cdot W(L, E)^{\beta_2}$  , or

193 (Eq. 4b)  $\phi(L) = \chi \cdot C(t) \cdot \kappa_3 \cdot L^{\beta_3}$  .

194 where  $\kappa_2 \cdot W(L, E)^{\beta_2}$  and  $\kappa_3 \cdot L^{\beta_3}$  are average food intake for a given body mass or body  
195 length, respectively. Typical values for the allometric exponents in fish are  $\beta_2 \sim 0.8$  and  
196  $\beta_3 \sim 2.5$  (Schmidt-Nielsen 1984).

### 197 **Energy allocation**

198 For every time-step, a proportion  $u(a, L, E, \phi)$  of net energy intake will be allocated to  
199 storage. The variable  $u$  is the core of this model, and when optimised over the entire life span  
200 it represents optimal life history strategies. As such,  $u$  balances the trade-off between growth  
201 and reproduction, and as such also integrates the effects of natural and fishing mortalities and  
202 the environment. Given  $u$ , the new state value of the energy stores in the next time-step is

203 (Eq. 5)  $E(t+1|u) = E(t) + u \cdot (\phi - MR) \cdot \delta_{\text{store}}$  ,  $E \leq E_{\text{max}}$  .

204 Here,  $\delta_{\text{store}}$  is the assimilation efficiency for the conversion of ingested energy to stores.  
205 The concept of the metabolic rate and the relationship between stored energy and spawned  
206 eggs embody energy losses at later steps; therefore this value is commonly higher than the  
207 assimilation efficiency for growth of somatic structures ( $\delta_{\text{growth}}$ ) below. The proportion  $(1 - u)$   
208 is allocated to somatic growth to a new length  $L(t+1|u)$

209 (Eq. 6) 
$$L(t+1|u) = \left[ L(t)^{3+\varepsilon} + \frac{(1-u) \cdot (\phi - MR) \cdot \delta_{\text{growth}} \cdot 100 \cdot L_{\text{std}}^\varepsilon}{K_{\text{min}} \cdot \rho_S} \right]^{\frac{1}{3+\varepsilon}},$$

210 
$$L(t+1) - L(t) \leq \Delta L_{\text{max}},$$

211 where  $\delta_{\text{growth}}$  is the efficiency with which available energy is assimilated into somatic  
 212 structures, and  $\rho_S$  ( $\text{J}\cdot\text{g}^{-1}$ ) is the energy density of somatic tissues and typically lower than the  
 213 energy density of stores. The equation basically states that growth is allometric with the  
 214 exponent  $(3+\varepsilon)$ , and new tissue is laid down according to available food, assimilation  
 215 efficiency and the energy density of somatic tissue. The constraint on maximum theoretical  
 216 growth rate,  $\Delta L_{\text{max}}$  ( $\text{cm}\cdot\text{t}^{-1}$ ), acts as an upper physiological limit for length increment per time  
 217 and can be parameterized from growth studies in food-unlimited immature fish.

## 218 **Reproduction and migration**

219 Feeding behaviour may be altered during reproduction and possibly also during the  
 220 migration to and from the spawning grounds. Therefore, the duration of these events must be  
 221 explicitly incorporated into the time-structure of the model. The time required for the  
 222 migration  $T_M(t)$  is the migration distance  $D_M$  (m) divided by the swimming speed through the  
 223 water masses:

224 (Eq. 7) 
$$T_M = \frac{D_M}{(U_S + U_C)},$$

225 where  $U_S$  ( $\text{m}\cdot\text{t}^{-1}$ ) is the average or typical swimming speed during the migration and  $U_C$   
 226 ( $\text{m}\cdot\text{t}^{-1}$ ) the speed of possible currents that have to be taken into consideration. If  $U_C \neq 0$  or the  
 227 migration route differs to and from the spawning grounds,  $T_M$  and the energetic cost of



228 migration  $E_M$  (J) have to be calculated separately for each direction. For species migrating in  
 229 groups or schools,  $U_S$  will often be identical for smaller and larger individuals.

230 The energetic costs of migration  $E_M$  (J) can then be found from:

231 (Eq. 8) 
$$E_M(W, L) = SMR(W) \cdot \left[ \left( \frac{\kappa_4 \cdot U_S^{1.5}}{L} + 1 \right) - Act_{std} \right] \cdot T_M, \quad E_M \geq 0,$$

232 The expression  $(\kappa_4 \cdot U_S^{1.5} \cdot L^{-1} + 1)$  determines an activity parameter similar to  $Act_{std}$  from  
 233 swimming speed and body size. Other formulations can be used, but a function on this form  
 234 proved to capture the dynamics of both body length and swimming speed in empirical data for  
 235 Atlantic cod (Strand et al. 2005) and other fish species (Nøttestad et al. 1999).

236 Stored energy is eventually spawned, and total egg production  $b$  is proportional to invested  
 237 energy (Marshall et al. 1999). If migration takes place, energy to fuel migration from  
 238 spawning grounds back to feeding areas has to be retained, although this constraint may be  
 239 modified to allow for semelparous life history strategies.

240 (Eq. 9) 
$$b(E) = \kappa_5 \cdot (E - E_M).$$

## 241 **Mortality**

242 A flexible mortality regime incorporating length-, size-, or age-specific natural mortality  
 243  $M$ , size- or stage-selective fisheries mortality  $F$  and additional mortality during migration and  
 244 spawning  $M_S$  can be specified. Mortality rates ( $t^{-1}$ ) are summed and survival probability  $S$   
 245 over a discrete time interval  $T$  (t) is then given by:

246 (Eq. 10) 
$$S = e^{-T(M+F+M_S)}.$$

247 If death by starvation is included, the above equation will apply for  $E > 0$ , while  $S = 0$   
 248 when  $E \leq 0$ . Details of the mortality regime used for calculations in this paper are given below  
 249 under the heading *Parameters for the Northeast Arctic cod stock*.

## 250 **Optimisation algorithm**

251 Optimal life-history strategies were optimized using dynamic programming (Houston and  
 252 McNamara 1999; Clark and Mangel 2000). Models of this type optimise a fitness function by  
 253 backward iteration through an individual's life history, starting at the maximum age and  
 254 constantly assuming that the individual acts optimally at every decision point in its future life.  
 255 A central point is that such models separate between the information available to the  
 256 individual (here its states) although other factors may affect its success (for instance the  
 257 development in food availability). Dynamic programming then finds the best response,  
 258 conditional on the information known by the individual, and averaged over possible  
 259 outcomes. The optimisation problem considered here is thus to find the allocation to  
 260 reproduction  $u(a,L,E,\phi)$  that maximises future expected reproductive value  $V(a,L,E,\phi)$   
 261 discounted by survival probability  $S$  for every combination of the four states (age  $a$ , body  
 262 length  $L$ , energy store  $E$ , and environment  $\phi$ ):

263 (Eq. 11)

$$264 \quad V(a, L, E, \phi) = \max_u \left\{ S \cdot \sum_{\phi(t+1)} P(\phi(t+1) | \phi(t)) \cdot [V(a+1, L(t+1|u), E(t+1|u), \phi(t+1)) + b(E)] \right\} .$$

265 Here  $P(\phi(t+1)|\phi(t))$  is the conditional probability of food availability in the next time step  
 266 given food availability in this time step. To find mean expected fitness one has to take the  
 267 sum over all possible states of food availability at time  $t+1$ . During the spawning season,  
 268 fitness values for both migrating and non-migrating individuals were calculated, and the

269 option yielding the highest fitness value was stored.

## 270 **Parameters for the Northeast Arctic cod stock**

271 The parameters below are selected to describe the physiology and ecology of the Northeast  
272 Arctic cod stock (summarised in Tab. 1). The time resolution is months to allow for seasonal  
273 variations in allocation patterns.

### 274 **Metabolic rate and food intake**

275 The equations for metabolic rate have been parameterised for Atlantic cod by Hansson et  
276 al. (1996). At an ambient temperature of 5 °C, and with a standard activity level set to  
277  $Act_{Std} = 1.25$  (Hansson et al. 1996), monthly metabolic rate MR ( $J \cdot month^{-1}$ ) was:

278 (Eq. 12)  $MR = SMR \cdot Act_{Std} = 2116 \cdot W(t)^{0.828}$ ,

279 where SMR is the standard monthly metabolic rate ( $J \cdot month^{-1}$ ).

280 Food intake at 5 °C was calculated according to Jobling (1988):

281 (Eq. 13a)  $\phi(L) = \chi(t) \cdot 276 \cdot L^{2.408}$ ,

282 by introducing additional stochasticity of the environment  $\chi(t)$ , auto-correlated in time and  
283 given by:

284 (Eq. 13b)  $\chi(t) = \bar{\chi} + C_1 \cdot (\chi(t-1) - \bar{\chi}) + C_2 \cdot N \cdot \sqrt{1 - C_1^2}$ ,

285 where  $N$  is a random number drawn from a standard normal distribution  $N(0,1)$ ,  $C_1 = 0.9$  is  
286 the auto-correlation coefficient,  $C_2 = 0.15$  scales the variance, and  $\bar{\chi} = 0.75$  is the mean of the

287 stochastic distribution. The feeding equation 13a was obtained in farmed cod fed to satiation  
288 (Jobling 1988) and  $\bar{\chi} = 1$  would correspond to the same feeding level in the model; by setting  
289  $\bar{\chi} = 0.75$  the mean feeding intake in the model is 25% less than for the farmed cod. Cod  
290 utilise many different prey species and can switch during unfavourable periods; there is also a  
291 maximum feeding rate that sets an upper limit for energy intake; for these reasons  $\chi(t)$  was  
292 constrained to fall between 0.3 and 1.5.

### 293 **Growth**

294 We used  $\varepsilon = 0.065$ , which was found from a log-log regression between mean length and  
295 weight for Northeast Arctic cod age-classes 1-12 measured in the field over the period 1978-  
296 2000 (ICES 2003). Maximum and minimum condition factors were set to  $K_{\min} = 0.75$  and  
297  $K_{\max} = 1.25$  for a standard length of  $L_{\text{std}} = 70$  cm; see Appendix 1 for justification. Maximum  
298 length increment was set to  $\Delta L_{\max} = 18 \text{ cm}\cdot\text{year}^{-1}$  and is a constant independent of length in  
299 this model, since field and experimental data show that length-growth is typically linear with  
300 time for food-unlimited immature cod, and decreases thereafter as a result of allocation to  
301 reproduction (e.g. Jørgensen 1992; Michalsen et al. 1998).

### 302 **Energy stores**

303 Together, muscle and liver stores vary between  $K_{\min}$  and  $K_{\max}$ , and the average energy  
304 density of full stores can be calculated provided that we know the energy content and relative  
305 contribution of each tissue type. Lipids are stored primarily in the liver, and the liver  
306 condition index (*LCI*) is liver weight expressed as percentage of total body mass. *LCI* reaches  
307 maximum values just prior to spawning; maximum monthly mean values for the Northeast  
308 Arctic cod stock are typically 7-8 % in early winter if food is abundant (Yaragina and  
309 Marshall 2000). A maximum value that can be obtained by the most successful individuals  
310 may exceed the average and was therefore set to  $LCI_{\max} = 9\%$ . Total liver energy density

311 ( $LEC$ ;  $J \cdot g^{-1}$ ) of full lipid stores in the liver is then given by (Lambert and Dutil 1997; Marshall  
312 et al. 1999):

313 (Eq. 14)  $LEC = 2.477 \cdot 10^4 \cdot \left(1 - e^{-0.52(LCI_{\max} - 0.48)}\right)$  .

314 The remainder of the weight increase due to storage is increased white muscle mass, which  
315 has an energy density of  $4130 J \cdot g^{-1}$  (Holdway and Beamish 1984, their table V). The average  
316 energy density of full stores can then be calculated to be  $\rho_E = 8700 J \cdot g^{-1}$ . For comparison,  
317 whole body energy density, which includes all tissue types and not only the lipid-rich energy  
318 stores, peaked at  $7000 J \cdot g^{-1}$  in a study of the chemical composition of cod (Holdway and  
319 Beamish 1984). The energy density of somatic tissues was furthermore calculated to  
320 be  $\rho_S = 4000 J \cdot g^{-1}$  from whole body energy content minus the liver for cod reared at  $5^\circ C$  in a  
321 study on chemical composition analysis of Atlantic cod (Holdway and Beamish 1984, their  
322 tables II, III and VI).

323 It is difficult to estimate energy loss in metabolic reactions, especially when the ingested  
324 molecules are only moderately rearranged before e.g. becoming part of the animal's stores. In  
325 general, half the energy in food can be made available as ATP (adenosine triphosphate), and  
326 maximum muscle efficiency (energy in ATP versus physical work done) is around 0.45  
327 (Alexander 2003), but we have not been able to find more exact determinations of overall  
328 metabolic pathways of relevance to this model. We set the proportion of ingested energy that  
329 was preserved when stored to  $\delta_{\text{store}} = 0.4$ . This value is relatively high because lipid and  
330 protein storage requires few biochemical rearrangements compared to somatic growth  
331 processes, and  $\delta_{\text{store}}$  accounts only for energy lost from ingestion to storage; energy losses  
332 during metabolism and production of eggs is taken into account in the empirical relationships  
333 in eqs. 9 and 12. Assuming further that the efficiency in converting energy from stores to eggs

334 is also 0.4, and that growing somatic structures such as bones and neural tissue is only half as  
335 efficient as the entire process from ingestion to egg production, we ended up with  
336  $\delta_{\text{growth}} = 0.08$  of the energy being preserved when used for somatic growth. These parameters  
337 were chosen also based on predicted growth patterns in terms of length and weight in the  
338 model.

### 339 **Migration and spawning**

340 Each January fish can either start migration in order to spawn, which occupies January  
341 through May, or stay at the feeding grounds. Atlantic cod eat little or nothing during the  
342 spawning season (Fordham and Trippel 1999). This has been simplified in the model, where  
343 there is no net gain in energy for spawning fish ( $\phi(W) = SMR \cdot Act_{\text{Std}}$ ). For calculations of  
344 energy consumption during spawning migrations, we used  $\kappa_4 = 320 \text{ cm} \cdot \text{s}^{1.5} \cdot \text{m}^{-1.5}$  (Strand et al.  
345 2005),  $U_S = 0.3 \text{ m} \cdot \text{s}^{-1}$  (Brander 1994), and  $U_C = 0.1 \text{ m} \cdot \text{s}^{-1}$  (Brander 1994). Because the current  
346 flows north along the Norwegian coast,  $(U_S + U_C)$  was used for estimating required time for  
347 the southward migration, while  $(U_S - U_C)$  was used for the migration north. The migration  
348 distance  $D_M = 7.8 \cdot 10^5 \text{ m}$  was measured on a nautical map. The required energy for migration  
349 was subtracted from the balance in one month, although the migration may take longer.

350 Stored energy was, for simplicity, spawned in one batch in March. Although there are  
351 indications that cod may adjust their spawning intensity between years to compensate for  
352 previous reproductive investments (Kjesbu et al. 1996), all stored energy except that required  
353 for the northbound migration was used for egg production in this model. Introducing a  
354 variable spawning intensity would mean to include one more trait in the model; deemed too  
355 complicated at present it suggests a potential direction in the future. In eq. 9,  $\kappa_5$  was set to  
356  $0.407 \cdot P_{\text{lipids}}$  (Marshall et al. 1999), where  $P_{\text{lipids}} = 0.63$  is the proportion of total energy stored  
357 that is stored as lipids in the liver and can be derived from the considerations on energy  
358 densities in different tissues above.

## 359 **Mortality**

360 Growth and maturation in the model are very sensitive to the choice of mortality regime.  
361 The mortalities in the spawner and the feeder fisheries were chosen to lie between the historic  
362 situation (before the onset of trawling), and the current harvesting regime. In evolutionary  
363 terms, this would imply that the resulting life history is partly adapted to the new and higher  
364 fisheries mortalities (either through contemporary evolution or through phenotypic plasticity  
365 that has evolved in response to variable mortality patterns in the past). The simulations in this  
366 paper used the following mortalities (all rates per year): natural mortality  $M = 0.25$ , increased  
367 mortality during the spawning/migration period  $M_S = 0.1$ , spawner fisheries mortality  
368  $F_S = 0.22$ , and feeder fisheries mortality  $F_F = 0.20$ . The spawning season lasts five months in  
369 this model, so annual mortality rates affecting only spawning individuals was spread evenly  
370 over these five months. The probability of surviving the next month was thus  
371  $S = e^{-[M/12+(M_S+F_S)/5]}$  when at the spawning grounds and  $S = e^{-(M+F_F)/12}$  when in the Barents  
372 Sea (from Eq. 10). The sensitivity to and effects of different mortality regimes are analysed  
373 together with skipped spawning in a companion paper (Jørgensen et al. this issue). We have  
374 not specified any size-dependent mortality.

## 375 **Initialisation and constraints**

376 The model starts from cod age 2, at which individuals were initiated with a length  
377  $L_{\min} = 25$  cm (Helle et al. 2002) and 30% energy stores in the forward simulation model.  
378 Maximum length had to be defined for the dynamic programming and was set to  $L_{\max} = 250$   
379 cm (Brander 1994; Svåsand et al. 1996); this is only a technical limit that has to be well above  
380 maximum lengths observed in cod to avoid boundary effects. The model does not incorporate  
381 age-specific rates of mortality (i.e. aging) apart from a maximum age of 25 years.

Table 1
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382 Many of the parameter values above can be used for other cod stocks. Mortalities and  
383 details regarding the spawning migration vary between stocks and have to be changed. The

384 physiology remains the same, except for the temperature dependence of food intake (Jobling  
385 1988) and metabolic rate (Hansson et al. 1996).

## 386 **Results**

### 387 **Comparisons with field data**

388 We illustrate how growth in the model compares with field data from the Barents Sea and  
389 the Lofoten area for the period 1978-2000 (Fig. 2; ICES 2003). To obtain the model's  
390 prediction of growth, a life history strategy was first found by optimisation using a  
391 representative set of parameters including natural and fisheries mortalities. The life history  
392 strategy was then simulated in an artificial population where population dynamics as well as  
393 patterns of growth and reproduction emerge. The desired individual and stock properties were  
394 recorded from the simulation; in this case weight- and length-at-age. For all ages, mean  
395 weight- and length-at-age predicted by the model fall within the range of observed mean  
396 weight- and length-at-age from field data, and there is no systematic bias.

Figure 2

397 The model also predicted the proportion of the stock that would be mature-at-length and -  
398 age (Fig. 3a and 3b, respectively). Mean length at 50% maturation was 78 cm and the  
399 corresponding age 7.5 years. For comparison, field data on the proportion mature-at-age from  
400 Lofoten and the Barents Sea combined (ICES 2003, their table 3.5) is also shown (Fig. 3b)  
401 and does not deviate notably from the model's predictions. The correspondence between the  
402 model and field data in terms of growth and reproduction forms the basis for further  
403 comparisons between the model and the Northeast Arctic cod stock.

Figure 3

### 404 **Individual trajectories of growth, allocation, and reproduction**

405 We provide a more detailed picture of how allocation between growth and reproduction  
406 shapes the life history of cod, by showing growth trajectories in terms of length- and weight-  
407 at-age, energy allocation, condition, food availability, survival probability, and the temporal



408 pattern of reproduction for one particular individual cod (Fig. 4). As immature, this individual  
409 prioritised growth, and length growth was almost linear with time (Fig. 4a). Allocation to  
410 stores was low, and only minor energy reserves were kept to balance the risk of starvation  
411 (Figs. 4b-c). In anticipation of reproduction, allocation shifted from growth to stores at age 7,  
412 approximately one year prior to the first spawning migration (Fig. 4b). The energy stored  
413 during this period prior to reproduction is later used for spawning migration and gonad  
414 development. As a consequence of increased allocation to stores, length growth slowed down  
415 and the condition factor increased rapidly. Egg production during the spawning season is also  
416 shown (Fig. 4d). Repeated reproductive events lead to similar patterns throughout the  
417 individual's life-time: allocation to stores prior to reproduction, rapid weight increase and no  
418 length growth, followed by reproduction. Curiously, this cod invested all its energy in growth  
419 also in some of the years after sexual maturation (e.g., at age 9 and partially at age 13), and  
420 skipped spawning entirely in those years. The phenomenon of skipped reproduction is studied  
421 more closely in Jørgensen et al. (this issue). Food availability (Fig. 4e) also influenced growth  
422 and reproduction. The variable food availability this cod experienced while immature lead to  
423 concomitant variations in growth rate (visible in Fig. 4a). Poor food availability also  
424 coincided with skipped spawning at age 13 and age 19. Survival probability until a given age  
425 dropped faster when at the spawning grounds since the combined mortality from fishing and  
426 reproduction is higher than the fishing mortality at the feeding grounds (Fig. 4f; note the  
427 logarithmic axis).

Figure 4

428 Fecundity will vary with the individual's size, its stored energy, and the size-dependent  
429 energetic cost of migration. Some relations with fecundity are shown to visualise these effects  
430 (Fig. 5). Maximum and average fecundity were increasing with age, but older individuals  
431 were also showing a higher variance (Fig. 5a). This is due to two reasons. First, a higher age  
432 will *per se* reduce the importance of growth and will tend to favour reproduction. Because of

Figure 5

433 the terminal age in the model, the expected future lifespan is lower at higher ages. This  
434 reduces the value of the future component of reproduction relative to the present, meaning  
435 that energy would best be used for reproduction. In economic terms, reproduction is low-risk  
436 instantaneous liquidation of available capital (stored energy), while growth is an investment in  
437 the future, subjected to a pay-off that is becoming increasingly more risky with higher age (or,  
438 in terms of the strategy, the devaluation rate is increasing with senescence). Second, older  
439 individuals are usually larger and will thus spend relatively less energy for the migration. This  
440 gives them more leeway than smaller fish, and while small fish were forced to have full  
441 energy stores to spawn, spawning fish of larger size would show higher variance in their  
442 stored energy.

443 The relationship between weight and fecundity was also highly variable (Fig. 5b), although  
444 less so for small fish (up to 7 kg) and for the very few large fish that were realised in the  
445 simulated population. The same trend was visible for the relationship between fecundity and  
446 length (Fig. 5c). It thus seems that age, weight, and length are all poor predictors of fecundity  
447 when used alone. Liver weight turned out to be a better predictor of individual fecundity (Fig.  
448 5d). The variance around this relationship was highest when liver weight was low, because  
449 small individuals with lipid-rich livers and a starved larger individual can have the same liver  
450 weight. In the model, liver energy content is the proximate mechanism that determines egg  
451 production; the variance around the relationships results because individuals in the population  
452 differ in age, size and stored energy (Fig. 5a-d).

### 453 **Stock and recruitment**

454 The picture looked somewhat different for egg production at the population level (Fig. 6),  
455 since variation at the individual level may cancel out or become amplified by correlations  
456 between individual states in the population. Variance was highest when plotted against total  
457 biomass of all sexually mature individuals (coefficient of variation for linear regression

Figure 6

458  $r^2 = 0.897$ ; Fig. 6a). Removing sexually mature individuals that did not engage in spawning  
459 removed a lot of the variance (Fig. 6b;  $r^2 = 0.995$ ). Liver weight was an even better predictor  
460 of egg production at the population level compared to its predictive ability for individual cod  
461 (Fig. 6c;  $r^2 = 0.986$ ). When the population's total egg production was plotted against total  
462 liver weight of only the individuals that were actually spawning, the points fell more or less  
463 onto a straight line (Fig. 6d;  $r^2 = 0.998$ ).

464 Maturity and fecundity relationships were also influenced by past food availability (Fig. 7;  
465 all values were from January, just prior to the spawning migration in the simulations). As  
466 predictor of mature biomass (defined as all fish that spawned for the first time this year or had  
467 spawned previously), the tightest relationship was obtained by averaging food availability  
468 over the last two years (Fig. 7a). For the stock's total egg production, the best relationship  
469 was obtained when mean food availability was averaged over the last year (Fig. 7b). The  
470 difference in time scales between these two relationships reflect that building gonads is a  
471 faster process than increasing mature biomass, which relies on both maturation and growth.

Figure 7

## 472 **Discussion**

473 We present here a model for energy allocation, parameterised for the Northeast Arctic cod.  
474 Since ingested energy can only be used once, the allocation pattern integrates trade-offs  
475 between life-history components and environmental factors and result in individual growth  
476 trajectories and maturation patterns. The model is complex but realistic. It adequately predicts  
477 complex life history phenomena such as indeterminate growth, skipped spawning and  
478 variability in age and size at maturation.

479 We make three assumptions: (i) that energy can only be used once; (ii) energy allocation is  
480 optimal at every point in life in the sense that it maximises fitness; and (iii) the fitness of an  
481 individual is approximated by its expected future reproductive value (true when density  
482 dependence acts early in life and the population is in equilibrium, Mylius and Diekmann

483 1995). This model makes predictions about life histories from first principles by finding  
484 optimal phenotypes. When compared with data, a fit between the predicted life histories and  
485 those realised in nature makes it likely that the most important assumptions are built into the  
486 optimality model, and that the model turn can be used to formulate or test hypotheses under a  
487 variety of ecological conditions (Sutherland 2005). The model provides a level of detail and  
488 realism that can readily be compared with field and experimental data, and the fit in terms of  
489 both growth and maturation are promising for further comparisons with field observations.

#### 490 **Abstract versus complex models**

491 Models with many parameters, such as the one presented here, are sometimes accused of  
492 being overly complex. Models can be complex in many ways, however. Although our model  
493 is rich in mathematical and mechanistic detail, it has a low level of abstraction. Abstract  
494 assumptions are replaced by a detailed and realistic formulation of energy allocation. We have  
495 aimed at parameters with sound biological meaning and included extensive arguments for the  
496 choice of parameter values. Species- and stock-specific parameters are required to make  
497 predictions about real-world scenarios. The results presented here are quite robust, as the  
498 patterns and results reported in this paper and Jørgensen et al. (this issue) are consistent  
499 throughout a wide range of parameter combinations.

500 Some of the properties of this model that resemble real-world dynamics, such as  
501 indeterminate growth, variation in age and size at maturation, and skipped spawning, do not  
502 occur if we switch off for instance the temporal variability in food intake. In a life history  
503 model for the Müller's pearlside (*Maurolicus muelleri*) stochasticity in the environment also  
504 lead to bet-hedging strategies and a two-year life cycle in stead of reproduction within one  
505 year only (Strand et al. 2002). Environmental variability is inherent in biological systems, and  
506 the observation that several real-world phenomena only occur when sufficient stochasticity is  
507 part of a model suggests that they are adaptations to a variable environment. Furthermore,

508 these adaptations affect population dynamics and ecological interactions. This basic insight is  
509 an argument for including stochasticity in models, especially where adaptations are  
510 concerned. Much of the rest of the complexity in this model is built around this stochasticity:  
511 size has to be included as a state because the variable environment will lead to temporal  
512 variations in size-at-age, and storing energy is a means of buffering environmental variation.

### 513 **Life history optimisation models**

514 This model aptly recaptures complex life history phenomena. Optimisation models have  
515 traditionally predicted determinate growth, where allocation should shift abruptly from  
516 growth to reproduction at a fixed point in life (e.g., Taborsky et al. 2003). The gradually  
517 increasing allocation to reproduction, as seen in the decelerating growth for individuals in our  
518 model, is common in nature but only rarely reproducible in models (but see Kozłowski and  
519 Teriokhin 1999; indeterminate growth is reviewed by Heino and Kaitala 1996). Our model  
520 also shows that cod may skip reproduction in some years, and this phenomenon of skipped  
521 reproduction has to our knowledge not previously been reproduced in models (Jørgensen et al.  
522 this issue). Growth in the model also fits well with observed growth patterns both in terms of  
523 length and weight at age when representative parameter values are used. In sum, we feel  
524 confident that the model behaves well and predicts reasonable and realistic growth and  
525 maturation patterns, and therefore that the results increase our understanding of the evolution  
526 of life history strategies in fish.

527 In principle, the model (as is typical for dynamic programming models) does not separate  
528 between phenotypic plasticity and evolutionary change – it simply finds the optimal life  
529 history strategies for a given set of parameters. The reaction norm concept describes the  
530 interaction between gene and environment, and is relevant for maturation processes since a  
531 fixed, genetically determined reaction norm can cause maturation to occur over a range of  
532 sizes and ages as the environment changes (Stearns and Koella 1986). The concept has been

533 extended to the probabilistic maturation reaction norm as a method to analyse maturation data  
534 (Heino et al. 2002). The rationale behind the reaction norm approach is that size at age, which  
535 naturally reflects past growth rate, should mean more for the timing of sexual maturation than  
536 size or age alone. Since age and length are states, our model includes the phenotypic plasticity  
537 described by the maturation reaction norm concept, and also uses stored energy as an  
538 additional dimension to fine-tune maturation dynamics.

### 539 **Stock and recruitment**

540 Finding promising proxies for recruitment is essential to successful management of our  
541 marine fish stocks. The exercise undertaken in this paper is a good illustration of how  
542 different proxies behave in a modelled stock where everything is in principle known.  
543 Fecundity is modelled strictly mechanistically, and is proportional to the amount of stored  
544 energy in the liver (Marshall et al. 1998; Marshall et al. 1999). Even though this is a  
545 deterministic relationship with no noise added, various measurable individual characteristics  
546 perform rather poorly as predictors of fecundity. The best predictor at the individual level –  
547 not surprising given the direct link between liver energy stores and fecundity – is liver weight.

548 The strict upper limit in all the graphs showing fecundity is due to a constraint specified in  
549 the model: individual condition factor could not exceed  $K_{\max}$ . The lower limit of fecundity is  
550 more variable, and emerges from trade-offs between many factors, e.g., at what combination  
551 of age and size should one mature, should one spawn although energy stores are not  
552 completely full, would these considerations be modified by the current availability of food  
553 etc. These trade-offs can be solved by the life history approach taken in this paper, and the  
554 result is that the lower limit of fecundity or total egg production resembles the variance one  
555 can see in real data.

556 In nature, similar trade-offs determine the maximum fecundity (i.e., the upper limit). For  
557 example, how does a bulging belly influence swimming efficiency or feeding (is there room

558 for digestion)? Will large gonads impair the functionality of the swim bladder (Ona 1990)? If  
559 so, what are the potential consequences? To what degree will activity level at the spawning  
560 grounds influence reproductive success? These trade-offs are harder to model because we  
561 know less about them.

562 By comparing Figures 5 and 6, it is promising to note that proxies at the population level  
563 are better predictors of the stock's total egg production than individual characteristics. In  
564 other words, the variable demography of the fish stock removes some of the variation inherent  
565 in relationships between individual characteristics and fecundity. A likely explanation for this  
566 is that reproduction is normally determined by a few abundant cohorts (e.g., first-, second-  
567 and third-time spawners). Over time, the variability of these cohorts between years is less than  
568 the total variation between individuals in the population as a whole, and this will tend to  
569 reduce the variance when egg production is plotted as a function of population-level  
570 characteristics.

571 At the individual level, liver weight was the best proxy, and this proxy performed well also  
572 at the population level. However, excluding the non-spawning part of the population provided  
573 even better predictions than using the total liver weight of the mature population. Skipped  
574 spawners will contribute to the stock's total liver weight without producing any eggs, and will  
575 therefore be the source of much of the variation. This goes for both the mature biomass–egg  
576 production relationship, as well as the relationship between total liver weight and egg  
577 production. The phenomenon of skipped spawning is studied in greater detail in Jørgensen et  
578 al. (this issue), providing an example application of this model to more complex questions of  
579 ecology and life history.

## 580 **The influence of density dependence**

581 With the optimisation technique used in this paper, dynamic programming, it is not  
582 straightforward to find optimal life history strategies when a population is regulated by

583 density dependence (Clark and Mangel 2000; Houston and McNamara 1999). The model can  
584 be turned into a dynamic game, but this would require a much more complex model  
585 (McNamara et al. 1997). Simulations of population dynamics, however, require that some  
586 regulatory mechanism controls population abundance, otherwise the population would go  
587 extinct or grow exponentially and infinitely. As a consequence, life history allocation  
588 strategies are found by optimisation without density dependence in this model, and the  
589 strategy thereafter simulated in a population where density dependence acts on juvenile  
590 survival. Before we can compare predictions from this model with results from density-  
591 dependent optimisation, we cannot with certainty conclude what the effects of density  
592 dependence are. The fit between the model's predictions and field data suggests that the  
593 model recaptures much of the ecological realism for this stock, even without adaptation to  
594 density dependence.

595 Alternatively, the life history problem outlined in our model could be solved using  
596 evolutionary modelling techniques that work also under density dependence. Adaptive  
597 dynamics is such a technique (Dieckmann and Law 1996). In practice, making assumptions  
598 about how an evolutionary change in one allocation value would incur correlated changes also  
599 in other values is exceedingly difficult for more than two or a few traits (compared to the 6.4  
600 million values in our model). With this, adaptive dynamics often got stuck in local optima that  
601 prevented further evolution (C. Jørgensen, B. Ernande and U. Dieckmann, pers. obs.). A  
602 second alternative is simulations of evolving population using genetic algorithms and  
603 artificial neural networks to approximate the allocation hypersurface (Huse et al. 1999). These  
604 models are, however, hard to trace: it is hard to ascertain when the neural network formulation  
605 allows sufficient detail in the allocation hypersurface, and whether globally optimal solutions  
606 are indeed found or not. We feel these uncertainties would be harder to accept than any



607 potential effects of density dependence, partly also because there is a weak tradition for  
608 including density dependence in models.

609 In conclusion, there is a promising agreement between field data and the model prediction  
610 of growth and maturation. In addition, the model gives a very realistic appearance of  
611 reproduction and other ecological interactions. Modelling tools such as this one can therefore  
612 be used for large-scale experiments that are logistically impossible or awkward in the field or  
613 lab. Because the entire population – structured by age, size and stored energy – is available  
614 throughout the stochastic simulation of population dynamics, a large array of various data can  
615 be explored in a more experiment-like way (Peck 2004). For instance, the model can be used  
616 to study effects of increased fishery mortalities: is the increasing mortality imposed by  
617 fisheries sufficient to induce life history evolution (e.g., Law and Grey 1989; Heino 1998;  
618 Olsen et al. 2004)? Another example, to which this model has already been applied, is skipped  
619 reproduction in fish (Jørgensen et al. this issue). The life history model suggests that the  
620 counter-intuitive phenomenon of skipped spawning may be more common than previously  
621 believed, and gives us the opportunity to study the underlying logic. The model provides a  
622 tool for large-scale investigations of the life history of cod in different ecological settings.  
623 Life history models, such as the one presented here, is a powerful tool for investigating both  
624 driving forces behind instantiated life history strategies, as well as assessing and predicting  
625 potential changes derived from altered external forcing such as fisheries and climate change.

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## 743 **Appendix 1**

### 744 **Justification for choice of minimum and maximum condition factors**

745 Growth in the model was sensitive to the choice of minimum and maximum condition  
746 factors. The following reasons for choosing  $K_{\min}$  and  $K_{\max}$  were therefore tightly coupled with  
747 sensitivity tests and comparisons with growth data. In an experiment following individual cod  
748 throughout the spawning season (length 56-87 cm; only females considered here), mean pre-  
749 spawning condition factor was 1.39 (range 1.19-1.75), while the average for spent cod was  
750 0.97 (range 0.81-1.13) (Fordham and Trippel 1999). Using these condition factors for  $K_{\min}$   
751 and  $K_{\max}$  in the model, however, gives higher condition factors and weight-at-age than is  
752 observed for the Northeast Arctic cod stock. This can be partly because eggs swell prior to  
753 spawning by taking up water (Tyler and Sumpter 1996; Fordham and Trippel 1999), which  
754 may artificially inflate condition factors for pre-spawning cod so that they no longer reflect  
755 the true size of energy stores. The extent of water uptake can be illustrated by the fact that  
756 total volume of eggs spawned was on average 150% of post-spawning body volume in the  
757 same study (Fordham and Trippel 1999). Also, cod were fed *ad libitum* throughout the  
758 spawning period in that study, and the easy access to food compared to natural conditions  
759 may have improved final condition. A somewhat lower maximum value,  $K_{\max} = 1.25$ , was  
760 therefore selected. In a starvation experiment, cod died when condition factors reached 0.44  
761 (range 0.36-0.56; length 31-55 cm), although liver energy stores were depleted before this  
762 (Dutil and Lambert 2000). The  $K_{\min}$  in this model should, however, reflect the condition at  
763 which routine energy stores are depleted, not the level to which severe food stress can atrophy  
764 muscle mass before death occurs. A value of  $K_{\min} = 0.75$  was therefore chosen through  
765 thorough testing since it reproduced appropriate weight-at-length compared to field data (e.g.  
766 Fig. 4.). Conditions factors in the model are given relative to a standard length  $L_{\text{std}} = 70$  cm,

767 which means that realised  $K_{\min}$  is in the range 0.71-0.74 for the lengths used in Dutil and  
768 Lambert (2000).



769 **Table 1.** Parameters used for Northeast Arctic cod (*Gadus morhua*) in a model for state-  
770 dependent energy allocation.

<b>Para- meter</b>	<b>Value and unit</b>	<b>Biological interpretation</b>
$\varepsilon$	0.065	Value of coefficient above 3 for allometric scaling between body mass and length
$K_{\min}$	$0.75 \text{ g}\cdot\text{cm}^{-3}$	Minimum condition factor at standard length $L_{\text{std}}$
$K_{\max}$	$1.25 \text{ g}\cdot\text{cm}^{-3}$	Maximum condition factor at standard length $L_{\text{std}}$
$L_{\text{std}}$	70 cm	Length for which $K_{\min}$ and $K_{\max}$ are defined
$\rho_E$	$8700 \text{ J}\cdot\text{g}^{-1}$	Energy density of muscle and liver energy stores
$\rho_S$	$4000 \text{ J}\cdot\text{g}^{-1}$	Energy density of somatic tissue
$Act_{\text{Std}}$	1.25	Proportional increase in metabolic rate due to activity
$\kappa_1$	1693 $\text{J}\cdot\text{g}^{-\beta_1}\cdot\text{month}^{-1}$	Coefficient of allometric metabolic function
$\beta_1$	0.828	Exponent of allometric metabolic function
$\kappa_2$	276 $\text{J}\cdot\text{cm}^{-\beta_2}\cdot\text{month}^{-1}$	Coefficient of allometric feeding function (of length)
$\beta_2$	2.408	Exponent of allometric feeding function (of length)
$\bar{\chi}$	0.75	Mean food intake relative to feeding function
$C_1$	0.9	Auto-correlation coefficient for environmental stochasticity
$C_2$	0.15	Scaling of environmental stochasticity
$\Delta L_{\max}$	$18 \text{ cm}\cdot\text{year}^{-1}$	Maximum growth rate
$D_M$	$7.8\cdot 10^5 \text{ m}$	Distance for spawning migration

$U_S$	$0.3 \text{ m}\cdot\text{s}^{-1}$	Swimming speed during spawning migration
$U_C$	$0.1 \text{ m}\cdot\text{s}^{-1}$	Speed of northwards current during spawning migration
$\kappa_4$	$320 \text{ cm}\cdot\text{s}^{1.5}\cdot\text{m}^{-1.5}$	Coefficient for empirical cost of swimming function
$P_{\text{lipids}}$	0.63	Proportion of total energy stored as lipids in liver
$LCI_{\text{max}}$	9%	Maximum weight of liver relative to body weight
$\delta_{\text{store}}$	0.4	Efficiency of storing ingested energy
$\delta_{\text{growth}}$	0.08	Efficiency of building somatic body mass from ingested energy
$\kappa_5$	$0.256 \text{ eggs}\cdot\text{J}^{-1}$	Conversion between stored energy and spawned eggs
$M$	$0.25 \text{ year}^{-1}$	Natural mortality
$M_S$	$0.1 \text{ year}^{-1}$	Increased mortality during spawning and migration
$F_F$	$0.20 \text{ year}^{-1}$	Feeder fisheries mortality
$F_S$	$0.22 \text{ year}^{-1}$	Spawner fisheries mortality
$a_{\text{max}}$	25 years	Maximum age
$a_{\text{min}}$	2 years	Age at which recruits are introduced in the model
$L_{\text{min}}$	25 cm	Length of recruits

771 **Figure captions**

772 **Figure 1.** Schematic overview over a life-history energy allocation model for the Northeast  
773 Arctic cod (*Gadus morhua*). Energy allocation and the states influencing it are shaded in grey.  
774 Black arrows indicate energy flow. The dotted line indicates that energy stores are drained in  
775 periods when food intake cannot sustain metabolic demands.

776 **Figure 2.** Predicted length and weight at age from a life history model for the Northeast  
777 Arctic cod (*Gadus morhua*) compared to field data. Grey points are data from the Barents Sea  
778 (mostly immature fish), while black open circles are from the Lofoten area (mostly mature  
779 fish). (a) Length (cm) at age (years). (b) Weight (kg) at age (years).

780 **Figure 3.** Maturity ogives from a life history model for the Northeast Arctic stock of  
781 Atlantic cod (*Gadus morhua*). (a) Proportion mature as a function of body length in cm. The  
782 equation for the logistic regression is  $y = 1/[1+\exp(-0.45\cdot(x-77.6))]$ . (b) Proportion mature as  
783 a function of age in years (black circles). Grey squares are field data for the Northeast Arctic  
784 cod stock for comparison (from ICES 2003). The equation for the logistic regression is  
785  $y = 1/[1+\exp(-1.7\cdot(x-7.5))]$ .

786 **Figure 4.** Growth trajectory and physiology for one individual female cod from a life  
787 history model for the Northeast Arctic cod *Gadus morhua*, simulated in a stochastic  
788 environment. The  $x$ -axis shows age and is common for all the graphs. Only one individual's  
789 life trajectory is shown in this figure. A population of individuals, each with a corresponding  
790 life trajectory, was simulated for the remaining results in this paper. This individual diverted  
791 energy towards stores at age 7, approximately one year prior to first spawning to prepare for  
792 sexual maturation. (a) Length (black line, left axis) and weight (grey line, right axis). (b)  
793 Allocation of available energy between energy stores (1) and growth (0). The line shows gaps  
794 because no energy is available for allocation during spawning migrations. (c) Fulton's  
795 condition factor (black line). The grey lines represent minimum and maximum condition

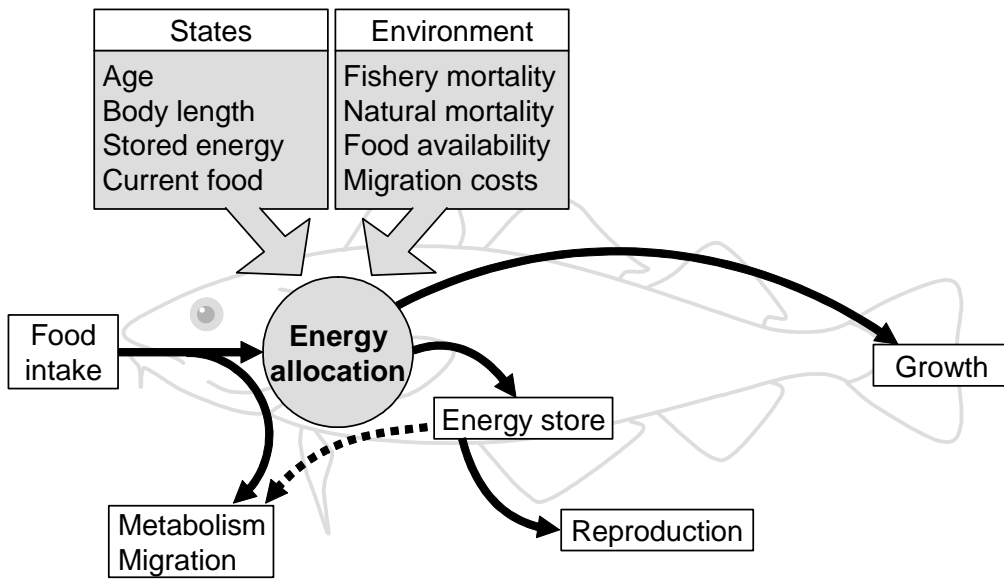
796 factors attainable at that length; these increase because body mass is proportional to length to  
797 the power of 3.065. (d) Number of eggs spawned (in millions). (e) Food availability in the  
798 stochastic environment measured relative to the mean. (f) Probability of survival until age  
799 (note the logarithmic y-axis).

800 **Figure 5.** Fecundity in relation to various individual characteristics. The y-axis is common  
801 for all graphs and show fecundity in million eggs. The results are from population simulation  
802 in a stochastic environment for 1000 years. (a) Fecundity vs. age (years). (b) Fecundity vs.  
803 body mass (kg). (c) Fecundity vs. body length (cm). (d) Fecundity vs. liver weight (g).

804 **Figure 6.** Comparison of population-level predictors of total egg production in the  
805 population. The y-axis is common for all the plots and shows the total egg production in the  
806 population. All axes are normalised to the mean, and the results are from population  
807 simulation in a stochastic environment for 1000 years. Coefficients of variation  $r^2$  are given  
808 for linear regressions on each data set. (a) Biomass of all sexually mature individuals  
809 (individuals that do not spawn but that have spawned previously are included) ( $r^2 = 0.897$ ).  
810 (b) Biomass of spawners only ( $r^2 = 0.995$ ). (c) Total liver weight of all sexually mature  
811 individuals (individuals that do not spawn but have spawned previously are included)  
812 ( $r^2 = 0.986$ ). (d) Total liver weight of spawners only ( $r^2 = 0.998$ ).

813 **Figure 7.** The influence of mean food availability on population characteristics in January  
814 (just before spawning season) in a life history model for the Northeast Arctic cod. All axes  
815 show values relative to the mean. Each point represents one year from 1000 years simulation  
816 of population dynamics. (a) In general, mature biomass was higher when mean food  
817 availability last two years was higher. Mature biomass includes effects of increased numbers  
818 of fish, increased proportion of mature fish, and increased condition. (b) Total egg production  
819 for the stock also showed a tendency to increase with increasing food availability.

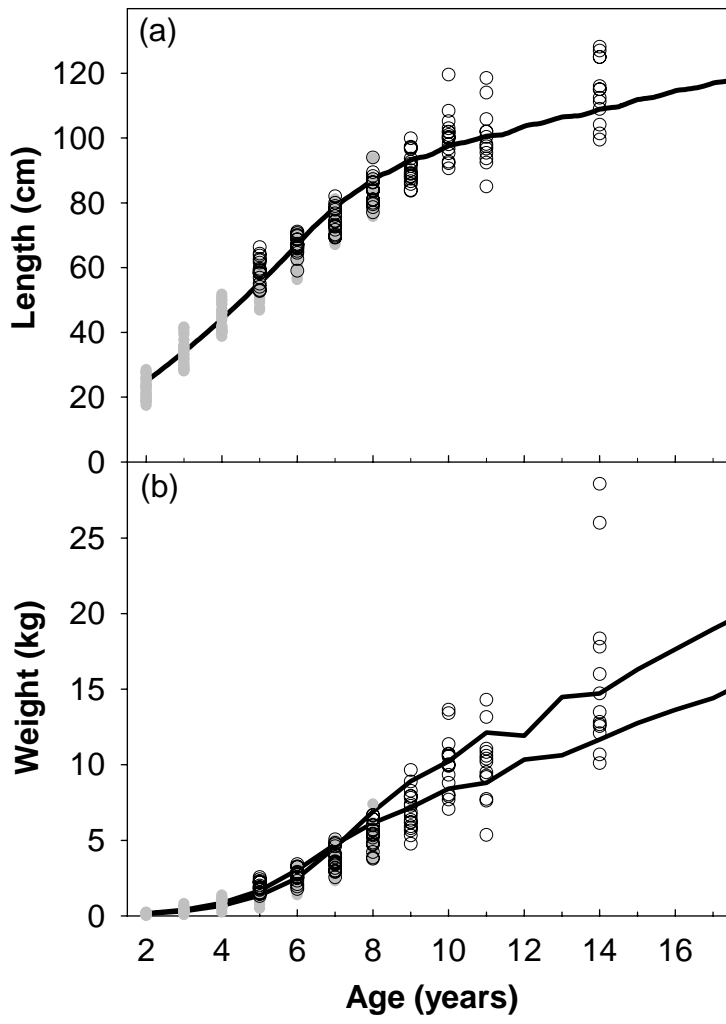




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821 Jørgensen and Fiksen. State-dependent energy allocation in cod (*Gadus morhua*)

822 **Figure 1**

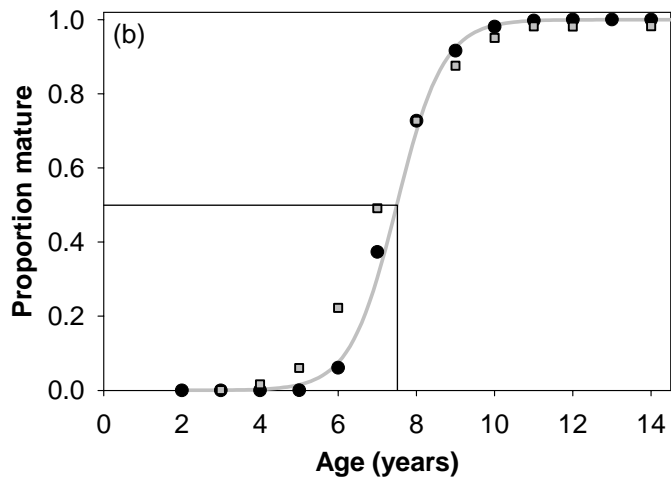
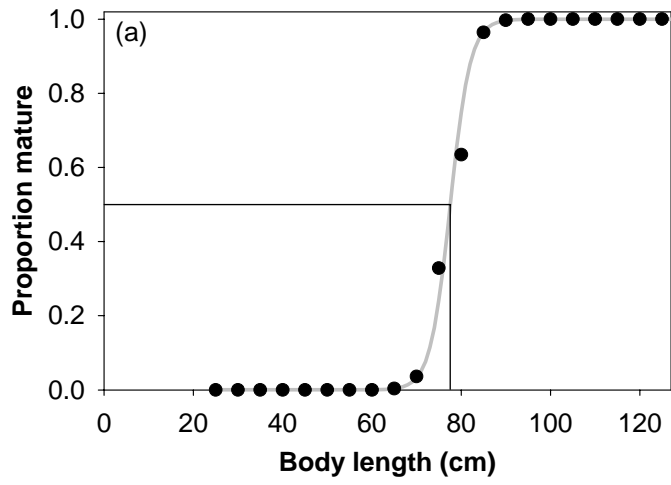


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824 Jørgensen and Fiksen. State-dependent energy allocation in cod (*Gadus morhua*)

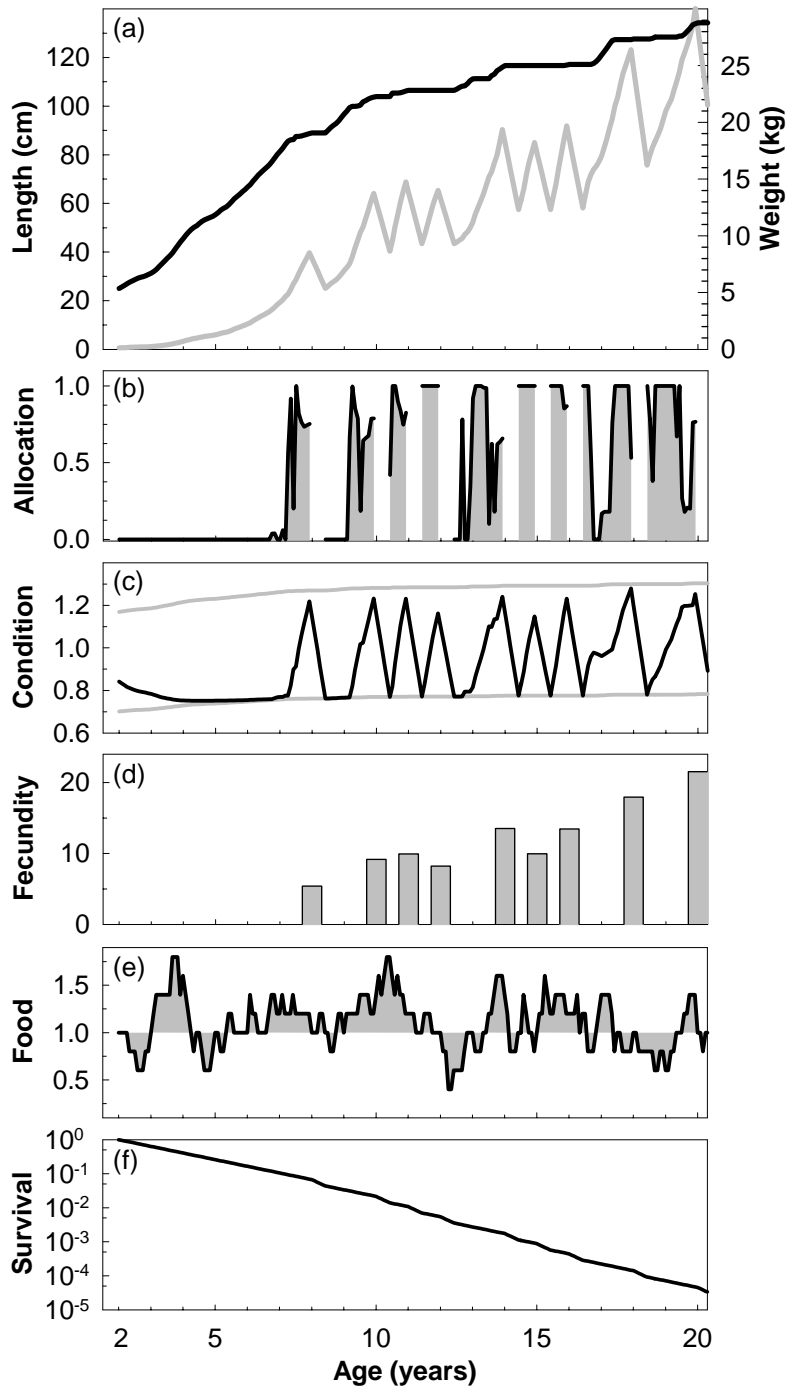
825 **Figure 2**



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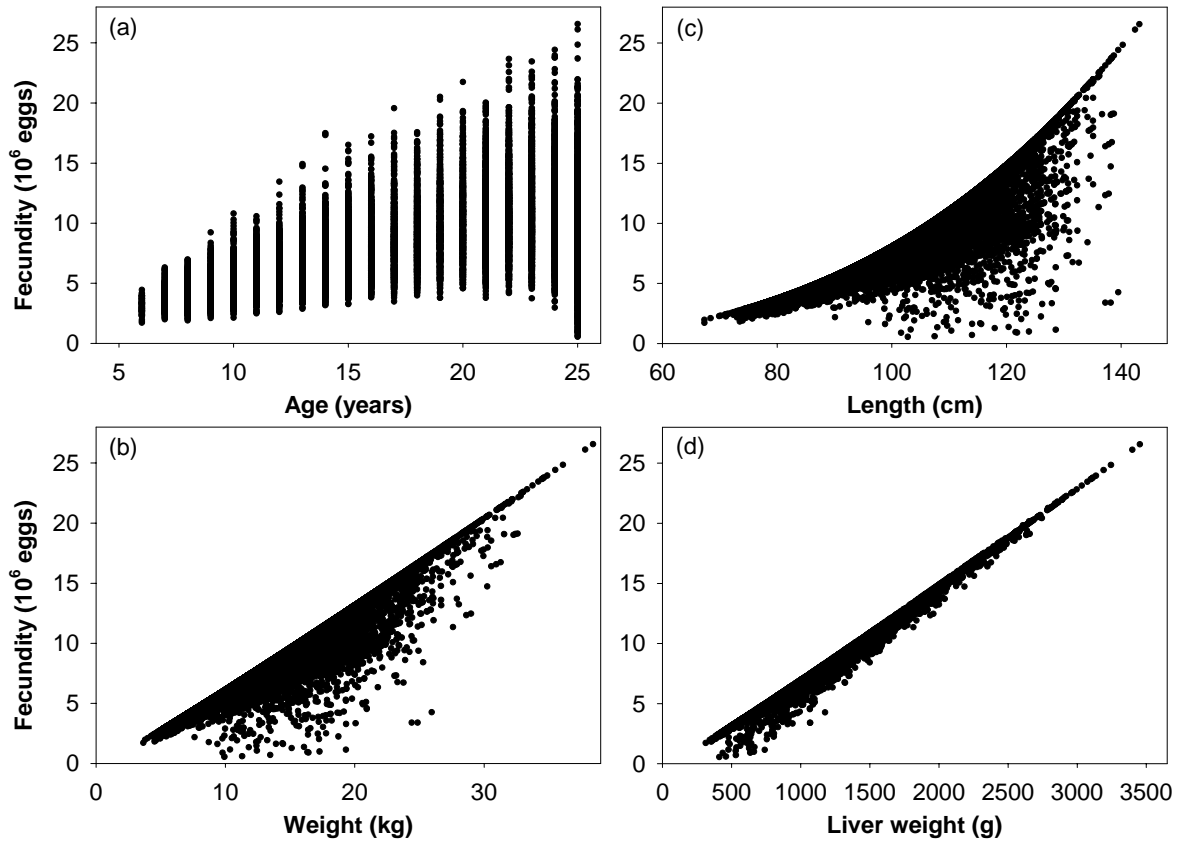
827 Jørgensen and Fiksen. State-dependent energy allocation in cod (*Gadus morhua*)

828 **Figure 3**



830 Jørgensen and Fiksen. State-dependent energy allocation in cod (*Gadus morhua*)

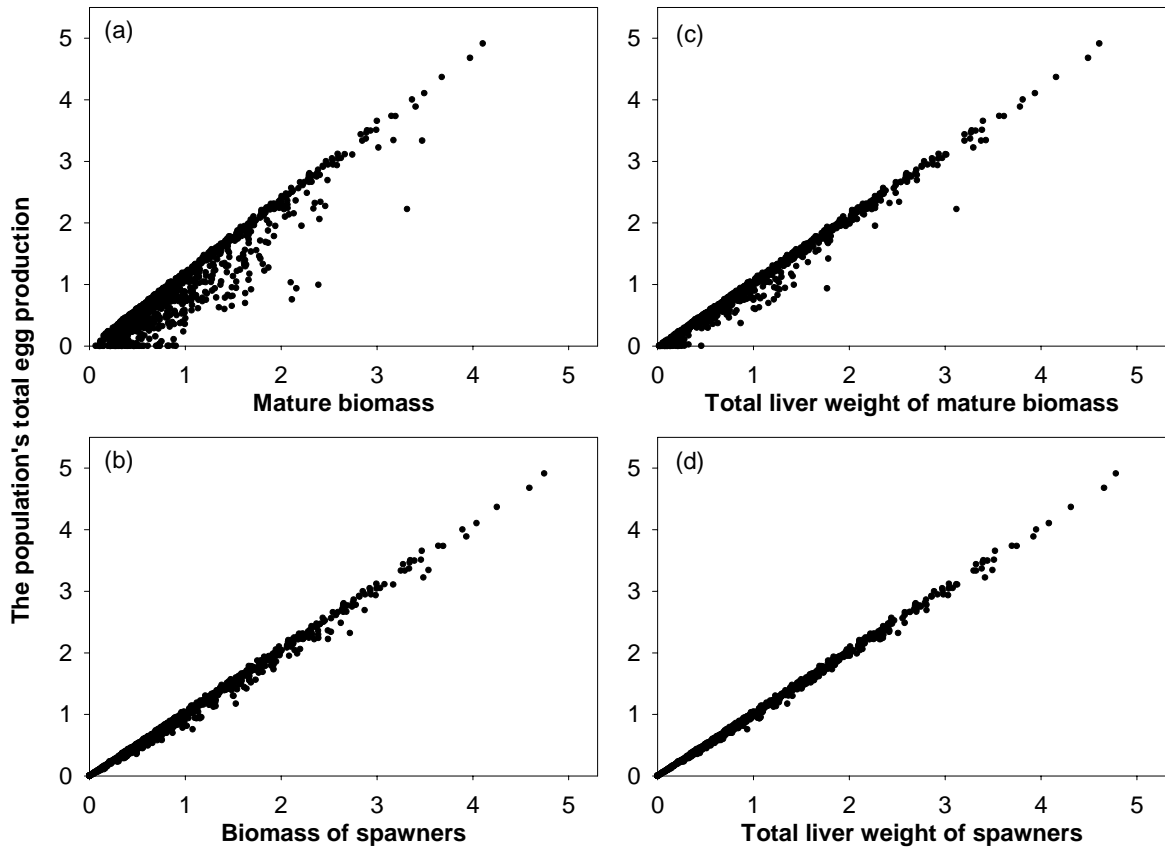
831 **Figure 4**



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833 Jørgensen and Fiksen. State-dependent energy allocation in cod (*Gadus morhua*)

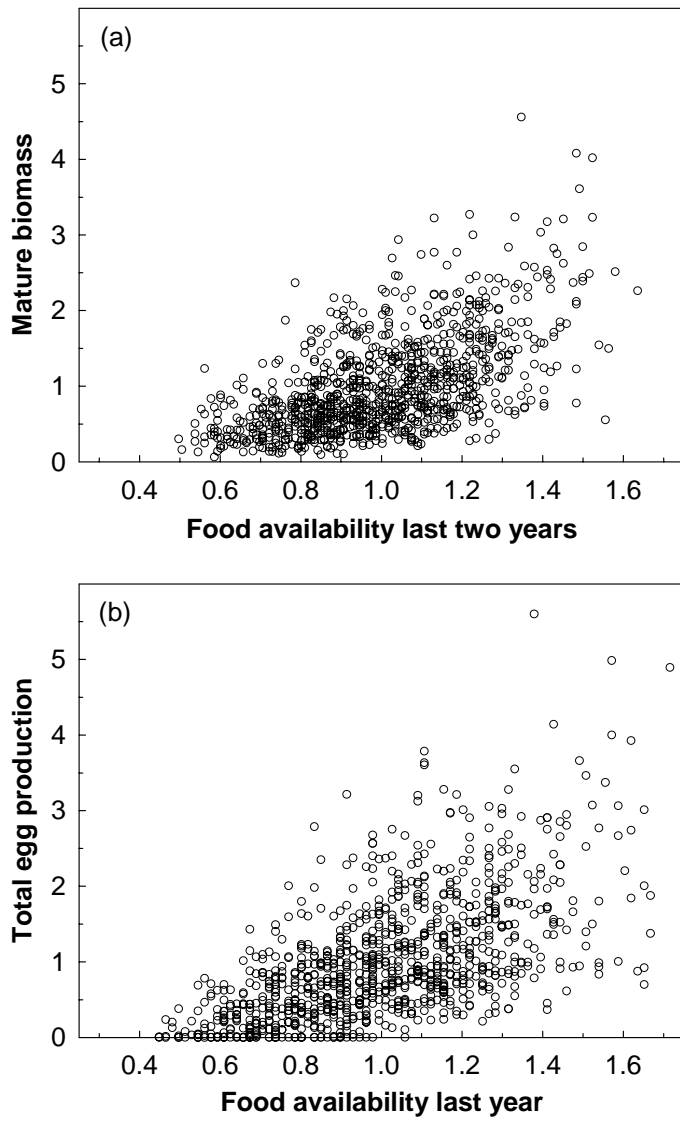
834 **Figure 5**



835



**Figure 6**



839 Jørgensen and Fiksen. State-dependent energy allocation in cod (*Gadus morhua*)

840 **Figure 7**