

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 ε 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_{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_{min} represents
165 the minimum body mass required for structures; death by starvation can be incorporated to
166 occur at K_{min} or with increasing probability as K_{min} is approached. Similarly, there is a limit
167 for how spherical the shape of an individual can be, and K_{max} is the maximum Fulton's
168 condition factor that includes W_{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_{max} . For
171 $\varepsilon \neq 0$, K_{min} and K_{max} must be specified for a given length L_{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, ρ_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)
$$E_{max}(L) = (K_{max} - K_{min}) \cdot \frac{\rho_E \cdot L^{3+\epsilon}}{100 \cdot L_{std}^\epsilon} .$$

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, κ_1 ($J \cdot g^{-\beta_1} \cdot t^{-1}$) is the coefficient and β_1 mass exponent of the allometric function.

187 **Environment**

188 Food intake ϕ ($J \cdot t^{-1}$) 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 χ 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, δ_{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 (δ_{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 δ_{growth} is the efficiency with which available energy is assimilated into somatic
 212 structures, and ρ_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, ΔL_{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 ϕ):

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 δ_{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, κ_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

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.

Para- meter	Value and unit	Biological interpretation
ε	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_{std}
K_{\max}	$1.25 \text{ g}\cdot\text{cm}^{-3}$	Maximum condition factor at standard length L_{std}
L_{std}	70 cm	Length for which K_{\min} and K_{\max} are defined
ρ_E	$8700 \text{ J}\cdot\text{g}^{-1}$	Energy density of muscle and liver energy stores
ρ_S	$4000 \text{ J}\cdot\text{g}^{-1}$	Energy density of somatic tissue
Act_{Std}	1.25	Proportional increase in metabolic rate due to activity
κ_1	1693 $\text{J}\cdot\text{g}^{-\beta_1}\cdot\text{month}^{-1}$	Coefficient of allometric metabolic function
β_1	0.828	Exponent of allometric metabolic function
κ_2	276 $\text{J}\cdot\text{cm}^{-\beta_2}\cdot\text{month}^{-1}$	Coefficient of allometric feeding function (of length)
β_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
ΔL_{\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
κ_4	$320 \text{ cm}\cdot\text{s}^{1.5}\cdot\text{m}^{-1.5}$	Coefficient for empirical cost of swimming function
P_{lipids}	0.63	Proportion of total energy stored as lipids in liver
LCI_{max}	9%	Maximum weight of liver relative to body weight
δ_{store}	0.4	Efficiency of storing ingested energy
δ_{growth}	0.08	Efficiency of building somatic body mass from ingested energy
κ_5	$0.256 \text{ eggs}\cdot\text{J}^{-1}$	Conversion between stored energy and spawned eggs
M	0.25 year^{-1}	Natural mortality
M_S	0.1 year^{-1}	Increased mortality during spawning and migration
F_F	0.20 year^{-1}	Feeder fisheries mortality
F_S	0.22 year^{-1}	Spawner fisheries mortality
a_{max}	25 years	Maximum age
a_{min}	2 years	Age at which recruits are introduced in the model
L_{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 $y = 1/[1+\exp(-1.7 \cdot (x-7.5))]$.

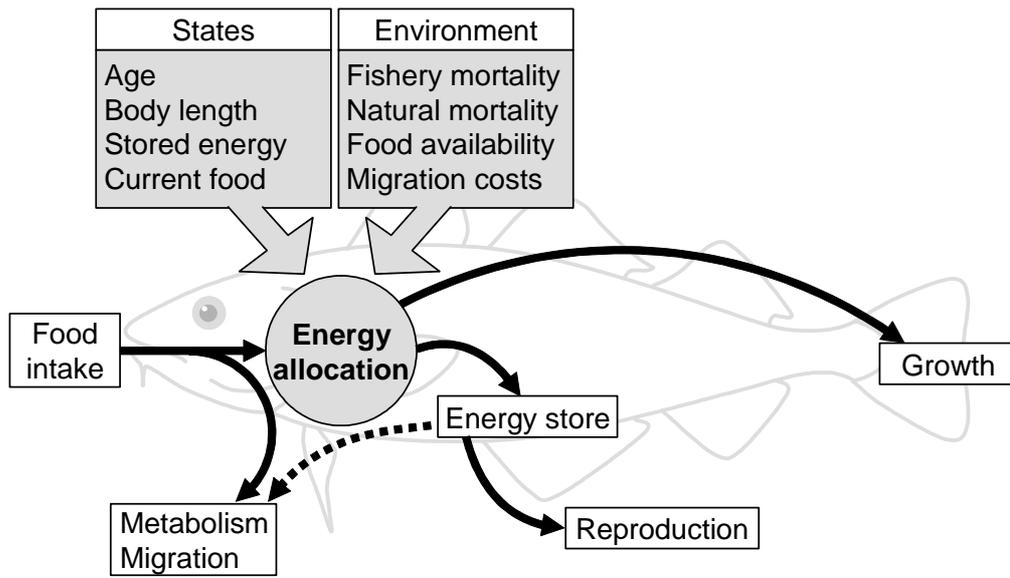
786 **Figure 4.** Growth trajectory and physiology for one individual female cod from a life
787 history model for the Northeast Arctic cod *Gadus morhua*, simulated in a stochastic
788 environment. The x -axis shows age and is common for all the graphs. Only one individual's
789 life trajectory is shown 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 ($r^2 = 0.998$).

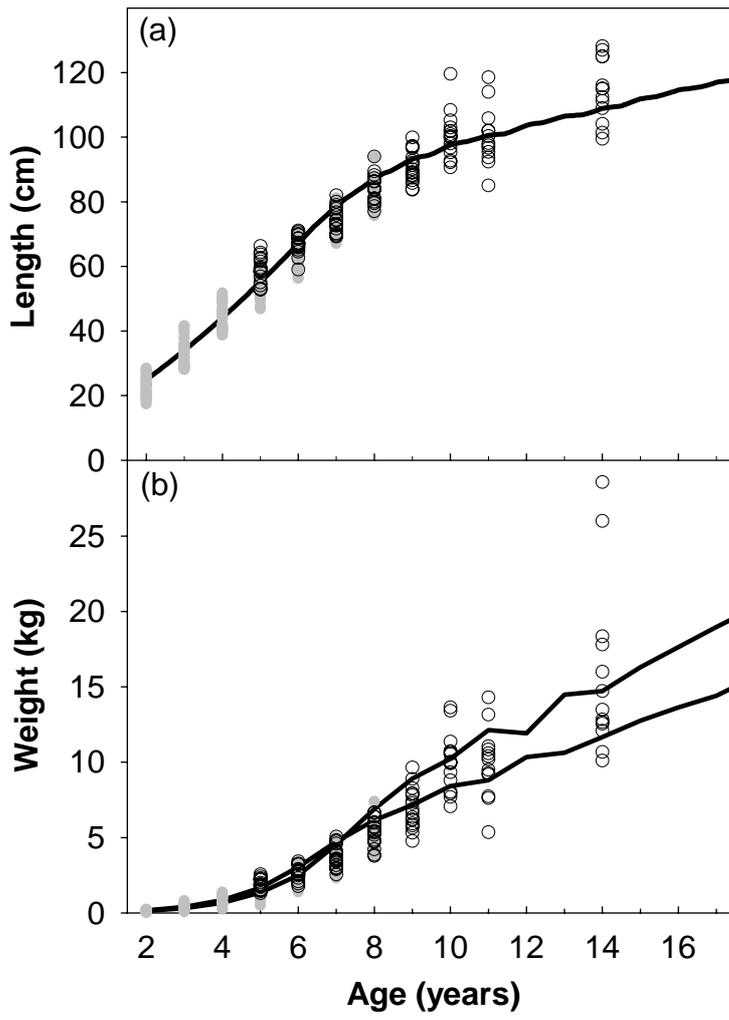
813 **Figure 7.** The influence of mean food availability on population characteristics in January
814 (just before spawning season) in a life history model for the Northeast Arctic cod. All axes
815 show values relative to the mean. Each point represents one year from 1000 years simulation
816 of population 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*)

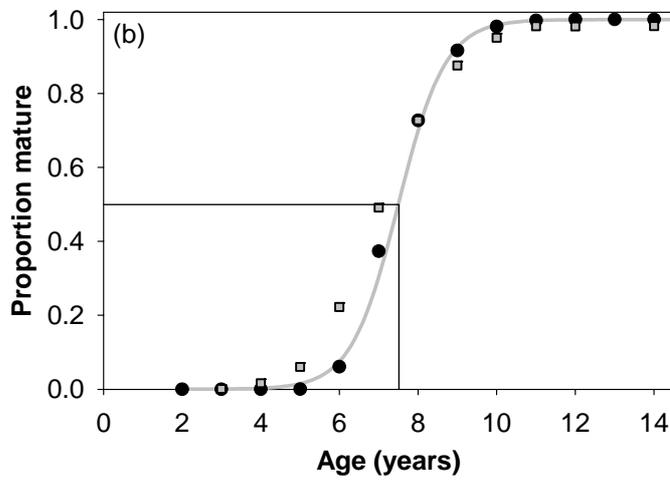
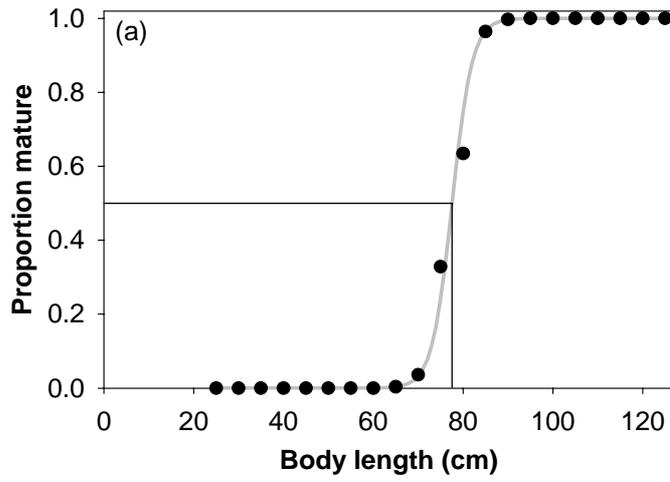
822 **Figure 1**



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

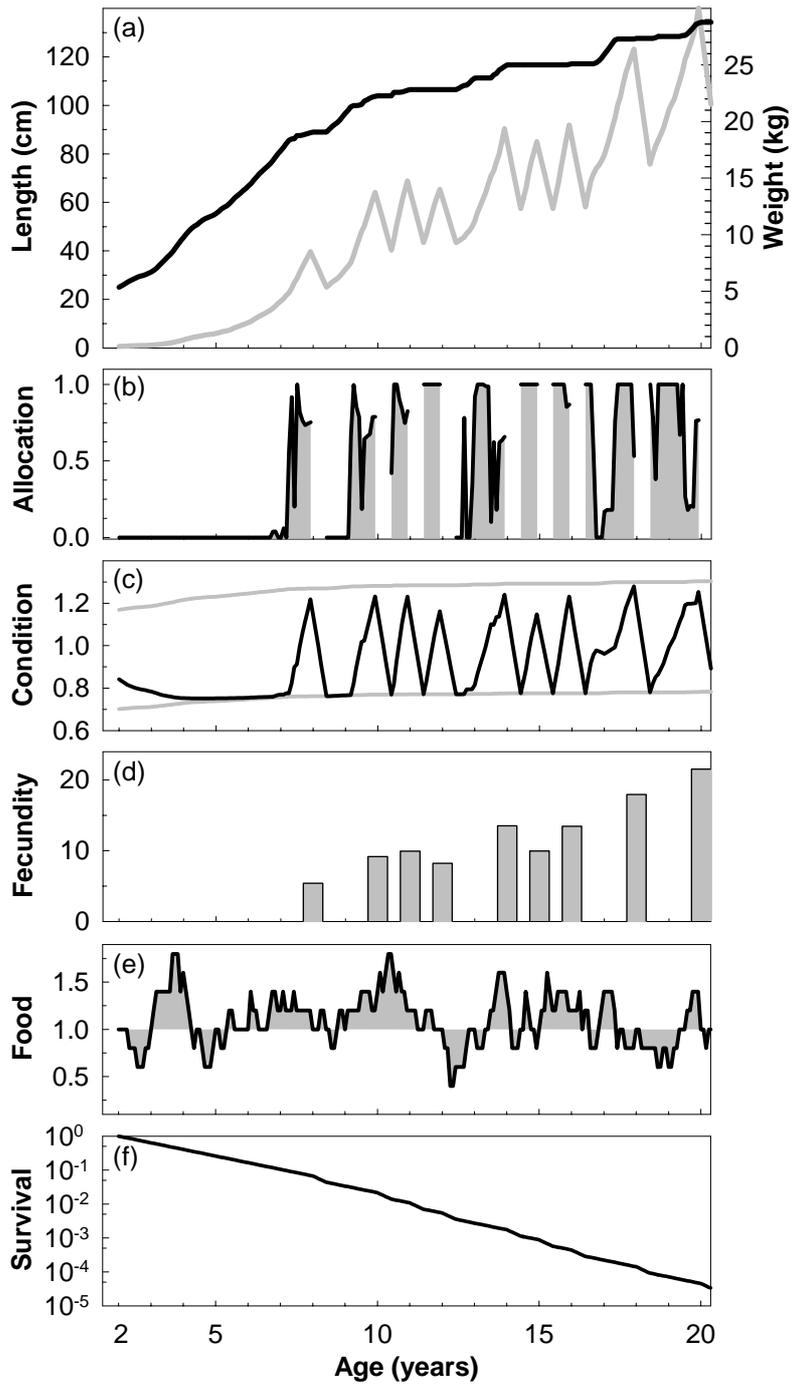
825 **Figure 2**



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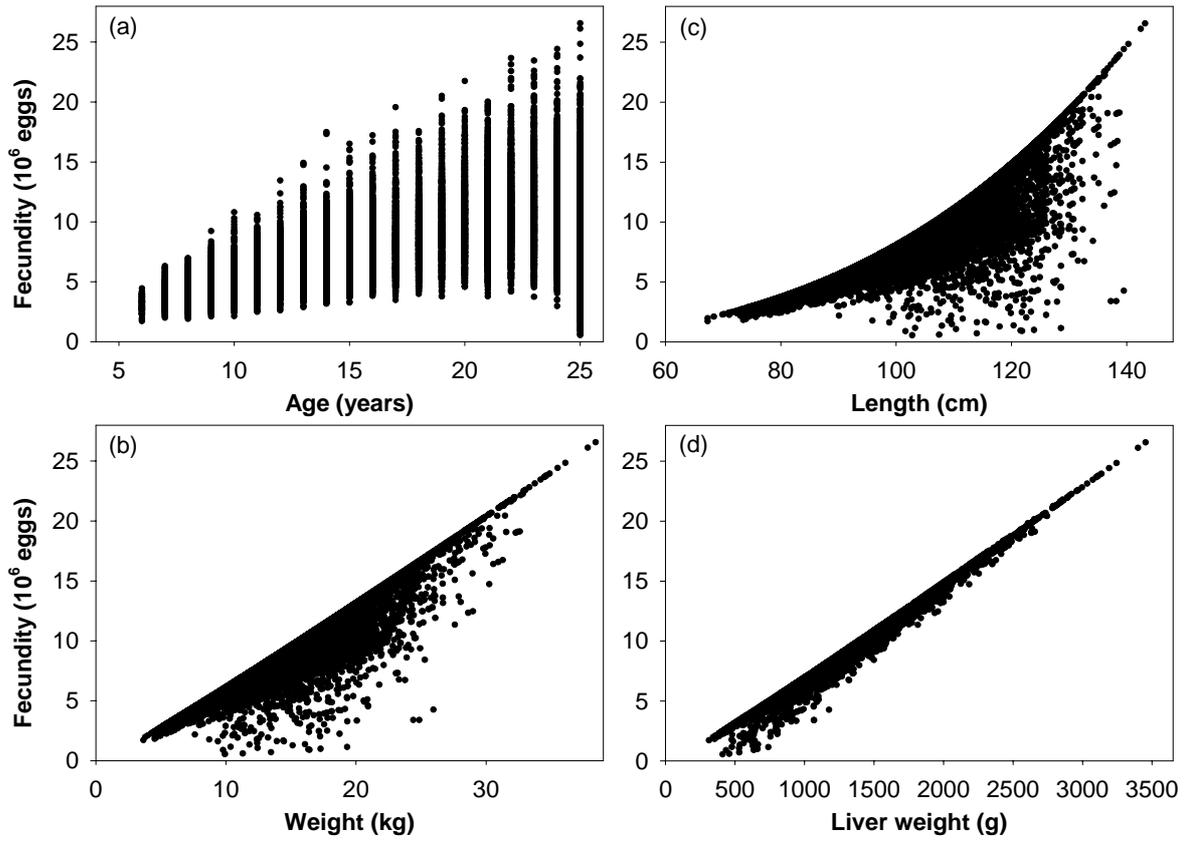
827 Jørgensen and Fiksen. State-dependent energy allocation in cod (*Gadus morhua*)

828 **Figure 3**



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

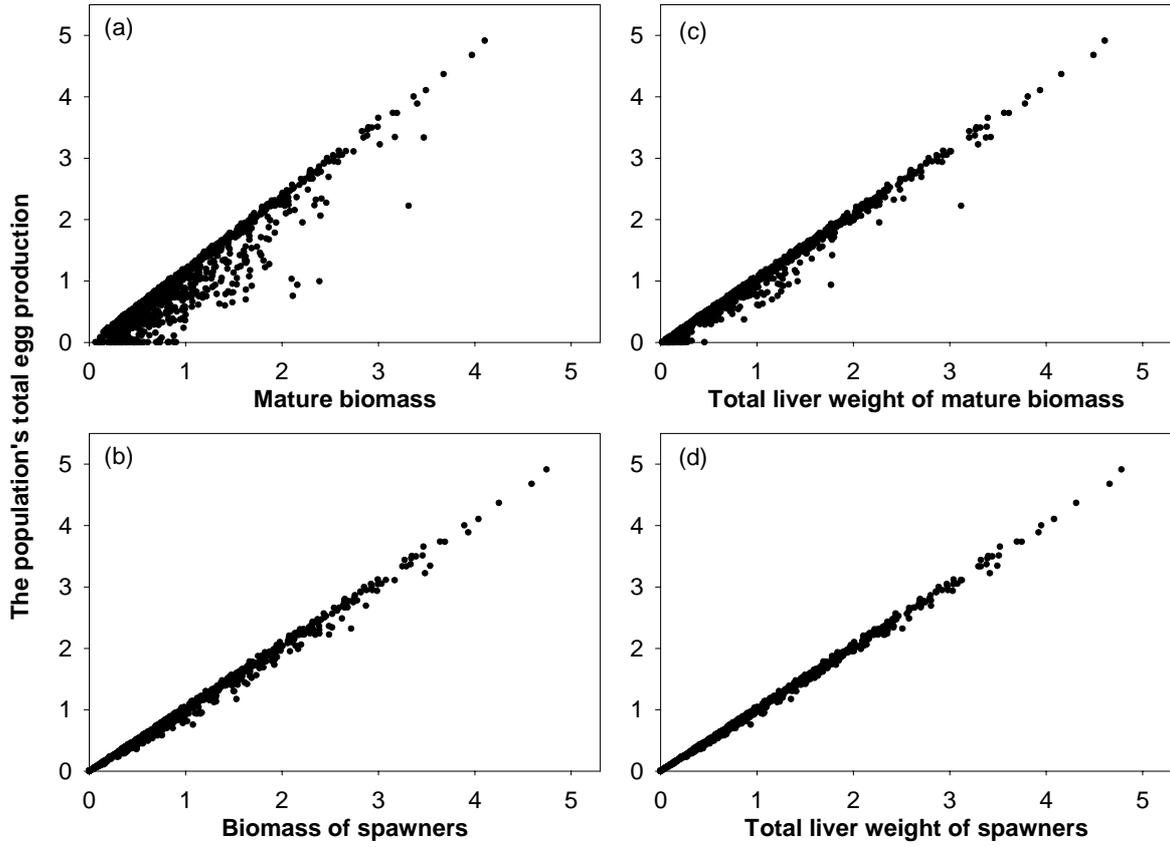
831 **Figure 4**



832

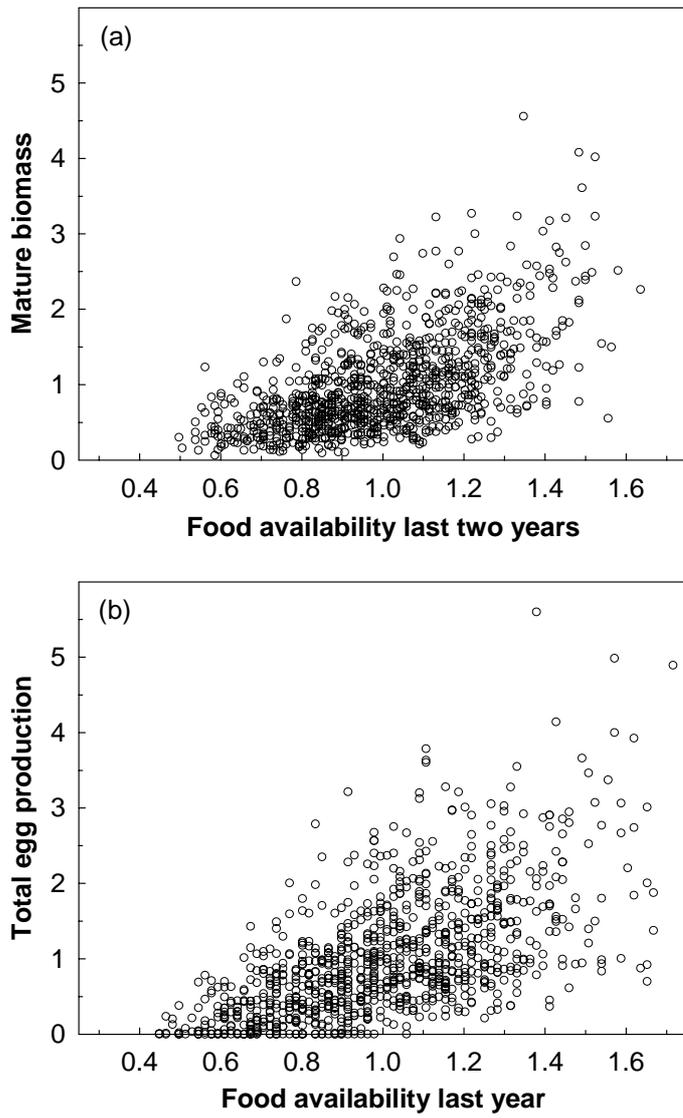
833 Jørgensen and Fiksen. State-dependent energy allocation in cod (*Gadus morhua*)

834 **Figure 5**



835

Figure 6



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

840 **Figure 7**