

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

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

Résumé : Les processus de croissance et de maturation sont ajustés à l'environnement externe qu'un individu est susceptible de connaître et, en particulier, à la disponibilité de la nourriture, au régime de mortalité et aux événements nécessaires pour compléter le cycle biologique. La compréhension des facteurs qui influencent les stratégies démographiques et, inversement, la connaissance de l'impact des changements de stratégie démographique sur la dynamique de population et les interactions écologiques sont essentielles pour interpréter l'écologie marine et les changements anthropiques contemporains. Nous présentons un modèle dépendant l'état qui optimise l'allocation de l'énergie tout au long de la vie chez les poissons itéropares. L'énergie peut être allouée à la croissance ou à la reproduction et elle varie en fonction de l'âge, de la longueur du corps et de l'énergie emmagasinée par l'individu, ainsi que de l'état de l'environnement. L'allocation et les processus physiologiques de croissance, de stockage d'énergie et de reproduction sont modélisés de manière mécaniste. Nous avons inséré dans le modèle les paramètres spécifiques à la morue franche (*Gadus morhua*), plus précisément au stock de morues du nord-est de l'Arctique. La croissance et la maturation prédites par le modèle s'ajustent bien aux observations de terrain; une étude plus poussée de la reproduction des morues dans le modèle nous amène à conclure que le modèle a la capacité de représenter des phénomènes complexes du cycle biologique, tels que la croissance indéterminée et les frayes omises et qu'il fournit ainsi un outil important qui peut fournir une meilleure compréhension des stratégies démographiques chez les poissons.

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Introduction

Energy use may be divided into three broad categories — survival, growth, and reproduction. These interests are often conflicting as they are crucial for fitness in different ways. When is an individual predicted to grow to increase future reproduction, and when to reproduce? A large size often means high reproductive success, but also low probability of survival until reproduction can finally take place. When is growth predicted to be determinate, and when indeterminate? When is survival probability predicted to influence the optimal adult size? And in the balance between foraging rate

and predation risk, when is an individual predicted to hide, and when to feed (Krebs and Davies 1993)?

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

Fisheries management is moving towards an ecosystem approach because ecological complexity confounds single-species management. At the same time, human-induced con-

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temporary evolution is identified as a potential driving force behind observed changes in many marine ecosystems (Stokes and Law 2000; Conover and Munch 2002; Olsen et al. 2004). Because life history theory is an obvious link between ecology and evolution, it provides a tool to predict growth, maturation, and behaviour as ecological forcing changes. Alterations in allocation strategies propagate from individual characteristics via population structure to ecological interactions within and between species. This implies that life history theory should be highly relevant for fisheries science, and understanding the logic of life history theory is an integral part of ecosystem management.

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

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

Earlier life history models investigating energy allocation in fish have used a fixed rule to describe lifelong allocation patterns: all available energy was allocated to growth up to a variable age at sexual maturation, and a fixed proportion of the energy was diverted to reproduction from then on to maximise reproductive value (Roff 1983; Law and Grey 1989; but see also Strand et al. 2002). These models have provided great insight into life history strategies and the evolutionary dynamics of harvested fish stocks, but time is now ripe to extend the analyses. Here, we investigate state-dependent energy allocation in a physiologically realistic model based on the Atlantic cod. Using four discretised state variables (age, length, stored energy, and food availability), our model allows for approximately 6.4 million independent values to describe a four-dimensional allocation hypersur-

face. In the strict sense, this is also a fixed rule, but the rule is so complex that it specifies what to do in nearly all situations that an individual can encounter throughout life.

Our aim is to formulate a flexible life history modelling tool. The high resolution enables seasonal patterns, as well as optimal size-, age-, and condition-dependent life history strategies, to emerge and introduces great flexibility with a sound biological basis into models of fish growth. The model makes very few life history assumptions, while letting optimisation tools exhibit the best patterns of growth and reproduction. This would also be the growth trajectories supposedly favoured by natural selection, assuming no constraints. We show that the model fits well with field data and experimental work and that it recaptures much of the ecological dynamics of the Northeast Arctic cod stock. In a companion paper, we apply the same model to analyse skipped spawning behaviour of cod (Jørgensen et al. 2006).

Model description

Purpose

We develop a state-dependent model that mechanistically describes energy allocation to growth and reproduction in fish. Because energy is a restricted resource, the life-long pattern in this allocation embodies many of the trade-offs that shape life history. The focus on energy allocation therefore fulfils the purpose of this model, which is to find the optimal life history under varying external forcing (e.g., fishing mortality, migration, and food availability). Throughout, we model the energy allocation processes as mechanistically correct as feasible, while retaining flexibility in how allocation can change with time and state. In this way we can use dynamic programming algorithms to find the optimal allocation pattern under the constraints given by the realistic and detailed description of physiology and ecology.

Structure

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

Processes

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

Concepts

Optimal energy allocation is determined for each state combination, with expected reproductive value as fitness measure. The result is a highly flexible multidimensional hypersurface that defines a life history strategy, described by 6.4 million independent points (each point corresponding to a particular combination of the four states). Because rewarding analyses are virtually impossible on such amounts of data directly, we simulated populations of fish realising such life history allocation strategies to let age-, size-, and condition-dependent patterns emerge at the individual and population level. A series of monthly energy allocations results in, e.g., a time series of growth, an age at sexual maturation, reproductive episodes with specific fecundities, and skipped spawning seasons (analysed separately in Jørgensen et al. (2006)). There is no interaction between individuals in the simulated population, and individuals only have information about the four individual states. Food availability is autocorrelated in time to allow for more extended periods of advantageous or unfavourable environment. In the forward population simulation, this is modelled as a stochastic process. Because optimal strategies may use the predictive power of an autocorrelated environment to fine tune allocation strategies (e.g., that a favourable environment is likely to persist for some time), current food availability was included as an extra state.

Initialisation

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

Input

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

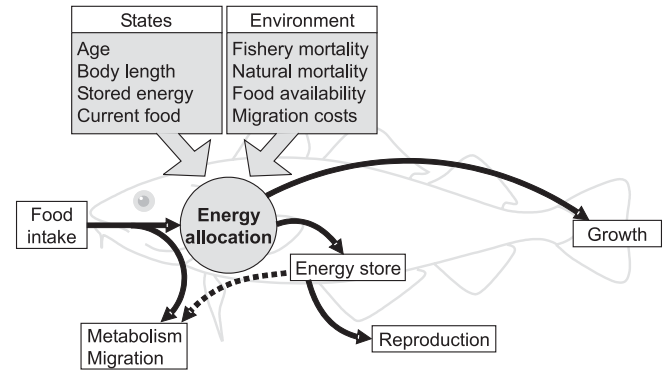
Submodels

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

Individual physiology

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

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



$$(1) \quad W_{\text{soma}}(L) = \frac{K_{\min} \cdot L^{3+\epsilon}}{100 \cdot L^{\epsilon}_{\text{std}}}$$

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

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

$$(2a) \quad W(L, E) = W_{\text{soma}}(L) + \frac{E}{\rho_E}$$

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

$$(2b) \quad E_{\text{max}}(L) = (K_{\max} - K_{\min}) \frac{\rho_E \cdot L^{3+\epsilon}}{100 \cdot L^{\epsilon}_{\text{std}}}$$

Energy expenditure is calculated according to the bioenergetics model by Hewett and Johnson (1992). Metabolic rate (MR ; $\text{J} \cdot \text{t}^{-1}$) is the product of the standard metabolic rate

(SMR; $J \cdot t^{-1}$) and an activity parameter Act_{std} to include a routine level of activity:

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

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

Environment

Food intake ϕ ($J \cdot t^{-1}$) is determined by food availability in the environment and a measure of body size (body mass (W ; g) or body length (L ; cm)). A stochastic function χ and seasonal cycles $C(t)$ can be incorporated to account for environmental variability in food availability. Feeding intake would thus be

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

or

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

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 length, respectively. Typical values for the allometric exponents in fish are $\beta_2 \sim 0.8$ and $\beta_3 \sim 2.5$ (Schmidt-Nielsen 1984).

Energy allocation

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

$$(5) \quad E(t + 1|u) = E(t) + u(\phi - MR) \delta_{store}, \quad E \leq E_{max}$$

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

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

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

where δ_{growth} is the efficiency with which available energy is assimilated into somatic structures, and ρ_S ($J \cdot g^{-1}$) is the energy density of somatic tissues and is typically lower than the energy density of stores. The equation basically states that growth is allometric with the exponent $(3 + \epsilon)$, and new tissue is laid down according to available food, assimilation efficiency, and the energy density of somatic tissue. The constraint on maximum theoretical growth rate, ΔL_{max} ($cm \cdot t^{-1}$), acts as an upper physiological limit for length increment per

time and can be parameterized from growth studies in food-unlimited immature fish.

Reproduction and migration

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

$$(7) \quad T_M = \frac{D_M}{(U_S + U_C)}$$

where U_S ($m \cdot t^{-1}$) is the average or typical swimming speed during the migration and U_C ($m \cdot t^{-1}$) is the speed of possible currents that have to be taken into consideration. If $U_C \neq 0$ or the migration route differs to and from the spawning grounds, then T_M and the energetic cost of migration, E_M (J), have to be calculated separately for each direction. For species migrating in groups or schools, U_S will often be identical for smaller and larger individuals.

E_M can then be found from

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

$$E_M \geq 0$$

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

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

$$(9) \quad b(E) = \kappa_5 (E - E_M)$$

Mortality

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

$$(10) \quad S = e^{-T(M+F+M_S)}$$

If death by starvation is included, the above equation will apply for $E > 0$, whereas $S = 0$ when $E \leq 0$. Details of the mortality regime used for calculations in this paper are given below (Parameters for the Northeast Arctic cod stock section).

Optimisation algorithm

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

$$(11) \quad V(a, L, E, \phi) = \max_u \left\{ b(E) + S \sum_{\phi(t+1)} P[\phi(t+1)|\phi(t)] \cdot V[a+1, L(t+1|u), E(t+1|u), \phi(t+1)] \right\}$$

Here $P[\phi(t+1)|\phi(t)]$ is the conditional probability of food availability in the next time step given food availability in this time step. To find mean expected fitness, one has to take the sum over all possible states of food availability at time $t+1$. During the spawning season, fitness values for both migrating and nonmigrating individuals were calculated, and the option yielding the highest fitness value was stored.

Parameters for the Northeast Arctic cod stock

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

Metabolic rate and food intake

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

$$(12) \quad MR = SMR \cdot Act_{std} = 2116 \cdot W(t)^{0.828}$$

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

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

$$(13a) \quad \phi(L) = \chi(t) \cdot 276 \cdot L^{2.408}$$

by introducing additional stochasticity of the environment, $\chi(t)$, autocorrelated in time and given by

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

where N is a random number drawn from a standard normal distribution $N(0,1)$, $C_1 = 0.9$ is the autocorrelation coefficient, $C_2 = 0.15$ scales the variance, and $\bar{\chi} = 0.75$ is the mean of the stochastic distribution. The feeding eq. 13a was obtained in farmed cod fed to satiation (Jobling 1988), and $\bar{\chi} = 1$ would correspond to the same feeding level in the model; by setting $\bar{\chi} = 0.75$, the mean feeding intake in the model is 25% less than for the farmed cod. Cod utilise many different prey species and can switch during unfavourable periods; there is also a maximum feeding rate that sets an upper limit for energy intake; for these reasons, $\chi(t)$ was constrained to fall between 0.3 and 1.5.

Growth

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

Energy stores

Together, muscle and liver stores vary between K_{min} and K_{max} , and the average energy density of full stores can be calculated provided that we know the energy content and relative contribution of each tissue type. Lipids are stored primarily in the liver, and the liver condition index (LCI) is liver weight expressed as percentage of total body mass. LCI reaches maximum values just prior to spawning; maximum monthly mean values for the Northeast Arctic cod stock are typically 7%–8% in early winter if food is abundant (Yaragina and Marshall 2000). A maximum value that can be obtained by the most successful individuals may exceed the average and was therefore set to $LCI_{max} = 9\%$. Total liver energy density (LEC; $J \cdot g^{-1}$) of full lipid stores in the liver is then given by (Lambert and Dutil 1997; Marshall et al. 1999):

$$(14) \quad LEC = 2.477 \cdot 10^4 (1 - e^{-0.52(LCI_{max} - 0.48)})$$

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

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

Parameter	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 g·cm ⁻³	Minimum condition factor at standard length L_{std}
K_{\max}	1.25 g·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 J·g ⁻¹	Energy density of muscle and liver energy stores
ρ_S	4000 J·g ⁻¹	Energy density of somatic tissue
Act_{std}	1.25	Proportional increase in metabolic rate as a result of activity
κ_1	1693 J·g ^{-β_1} ·month ⁻¹	Coefficient of allometric metabolic function
β_1	0.828	Exponent of allometric metabolic function
κ_2	276 J·cm ^{-β_2} ·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	Autocorrelation coefficient for environmental stochasticity
C_2	0.15	Scaling of environmental stochasticity
ΔL_{max}	18 cm·year ⁻¹	Maximum growth rate
D_M	7.8·10 ⁵ m	Distance for spawning migration
U_S	0.3 m·s ⁻¹	Swimming speed during spawning migration
U_C	0.1 m·s ⁻¹	Speed of northwards current during spawning migration
κ_4	320 cm·s ^{1.5} ·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 eggs·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

It is difficult to estimate energy loss in metabolic reactions, especially when the ingested molecules are only moderately rearranged before, e.g., becoming part of the animal's stores. In general, half the energy in food can be made available as ATP (adenosine triphosphate), and maximum muscle efficiency (energy in ATP versus physical work done) is around 0.45 (Alexander 2003), but we have not been able to find more exact determinations of overall metabolic pathways of relevance to this model. We set the proportion of ingested energy that was preserved when stored to $\delta_{\text{store}} = 0.4$. This value is relatively high because lipid and protein storage requires few biochemical rearrangements compared with somatic growth processes, and δ_{store} accounts only for energy lost from ingestion to storage; energy losses during metabolism and production of eggs are taken into account in the empirical relationships in eqs. 9 and 12. Assuming further that the efficiency in converting energy from stores to eggs is also 0.4 and that growing somatic structures such as bones and neural tissue is only half as efficient as the entire process from ingestion to egg production, we ended up with $\delta_{\text{growth}} = 0.08$ of the energy being preserved when used for somatic growth. These

parameters were chosen also based on predicted growth patterns in terms of length and weight in the model.

Migration and spawning

Each January, fish can either start migration in order to spawn, which occupies January through May, or stay at the feeding grounds. Atlantic cod eat little or nothing during the spawning season (Fordham and Trippel 1999). This has been simplified, and in the model, there is no net gain in energy for fish during migration and spawning ($\phi(W)$ is set to equal $\text{SMR} \cdot \text{Act}_{\text{std}}$). For calculations of 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. 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 flows north along the Norwegian coast, ($U_S + U_C$) was used for estimating required time for the southward migration, whereas ($U_S - U_C$) was used for the migration north. The migration distance $D_M = 7.8 \cdot 10^5 \text{ m}$ was measured on a nautical map. The required energy for migration was subtracted from the balance in 1 month, although the migration may take longer.

Stored energy was, for simplicity, spawned in one batch in March. Although there are indications that cod may adjust their spawning intensity between years to compensate for previous reproductive investments (Kjesbu et al. 1996), all stored energy except that required for the northbound migration was used for egg production in this model. Introducing a variable spawning intensity would mean including one more trait in the model; deemed too complicated at present, it suggests a potential direction in the future. In eq. 9, κ_5 was set to $0.407 \cdot P_{\text{lipids}}$ (Marshall et al. 1999), where $P_{\text{lipids}} = 0.63$ is the proportion of total energy stored that is stored as lipids in the liver and can be derived from the considerations on energy densities in different tissues above.

Mortality

Growth and maturation in the model are very sensitive to the choice of mortality regime. The mortalities in the spawner and feeder fisheries were chosen to lie between the historic situation (before the onset of trawling) and the current harvesting regime. In evolutionary terms, this would imply that the resulting life history is partly adapted to the new, higher fisheries mortalities (either through contemporary evolution or through phenotypic plasticity that has evolved in response to variable mortality patterns in the past). The simulations in this paper used the following mortalities (all rates per year): natural mortality $M = 0.25$, increased mortality during the spawning (migration) period $M_S = 0.1$, spawner fisheries mortality $F_S = 0.22$, and feeder fisheries mortality $F_F = 0.20$. The spawning season lasts 5 months in this model, so annual mortality rates affecting only spawning individuals was spread evenly over these 5 months. The probability of surviving the next month was thus $S = e^{-[M/12 + (M_S + F_S)/5]}$ when at the spawning grounds and $S = e^{-(M + F_F)/12}$ when in the Barents Sea (from eq. 10). The sensitivity to and effects of different mortality regimes are analysed together with skipped spawning in a companion paper (Jørgensen et al. 2006). We have not specified any size-dependent mortality.

Initialisation and constraints

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

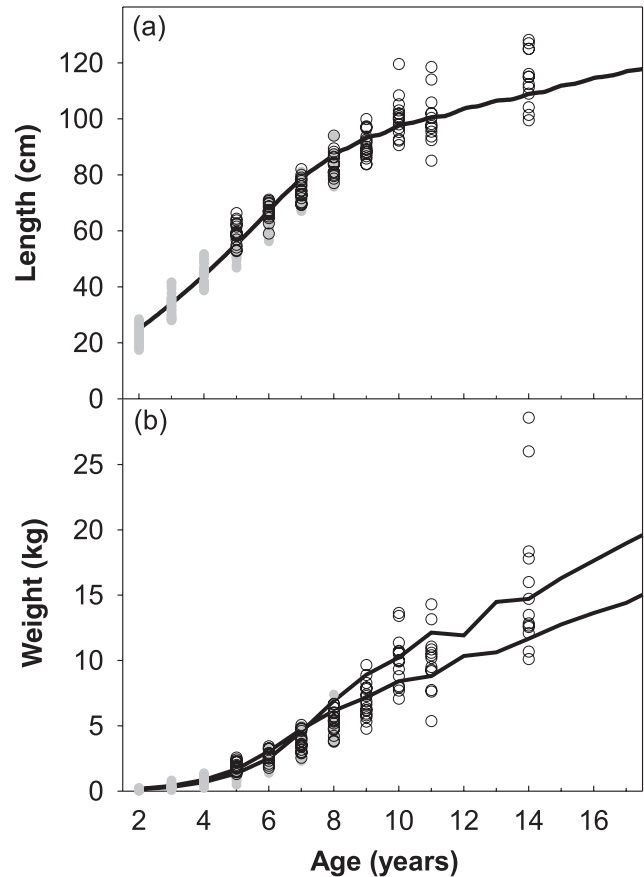
Many of the parameter values above can be used for other cod stocks. Mortalities and details regarding the spawning migration vary between stocks and have to be changed. The physiology remains the same, except for the temperature dependence of food intake (Jobling 1988) and metabolic rate (Hansson et al. 1996).

Results

Comparisons with field data

We illustrate how growth in the model compares with field data from the Barents Sea and the Lofoten area for the

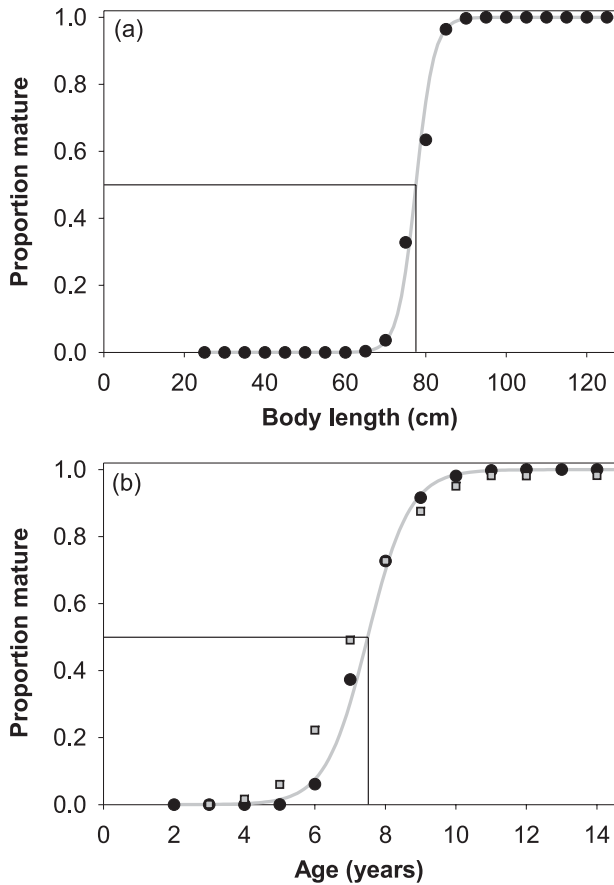
Fig. 2. Predicted length- and weight-at-age from a life history model for the Northeast Arctic cod (*Gadus morhua*) compared with field data. Shaded points are data from the Barents Sea (mostly immature fish), and open circles are from the Lofoten area (mostly mature fish). (a) Length (cm) at age (years). (b) Weight (kg) at age (years).



period 1978–2000 (Fig. 2; ICES 2003). To obtain the model's prediction of growth, a life history strategy was first found by optimisation using a representative set of parameters including natural and fisheries mortalities. The life history strategy was then simulated in an artificial population where population dynamics, as well as patterns of growth and reproduction, emerge. The desired individual and stock properties were recorded from the simulation, in this case, weight- and length-at-age predicted by the model fall within the range of observed mean weight- and length-at-age from field data, and there is no systematic bias.

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

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



Individual trajectories of growth, allocation, and reproduction

We provide a more detailed picture of how allocation between growth and reproduction shapes the life history of cod by showing growth trajectories in terms of length- and weight-at-age, energy allocation, condition, food availability, survival probability, and the temporal pattern of reproduction for one particular individual cod (Fig. 4). As an immature cod, this individual prioritised growth, and length growth was almost linear with time (Fig. 4a). Allocation to stores was low, and only minor energy reserves were kept to balance the risk of starvation (Figs. 4b–4c). In anticipation of reproduction, allocation shifted from growth to stores at age 7, approximately 1 year prior to the first spawning migration (Fig. 4b). The energy stored during this period before reproduction is later used for spawning migration and gonad development. As a consequence of increased allocation to stores, length growth slowed down and the condition factor increased rapidly. Egg production during the spawning season is also shown (Fig. 4d). Repeated reproductive events lead to similar patterns throughout the individual’s lifetime:

Fig. 4. Growth trajectory and physiology for one individual female cod from a life history model for the Northeast Arctic cod (*Gadus morhua*), simulated in a stochastic environment. The x axis shows age and is common for all the graphs. Only one individual’s life trajectory is shown in this figure. A population of individuals, each with a corresponding life trajectory, was simulated for the remaining results in this paper. This individual diverted energy towards stores at age 7, approximately 1 year before first spawning to prepare for sexual maturation. (a) Length (black line, left axis) and weight (shaded line, right axis). (b) Allocation of available energy between energy stores (1) and growth (0). The line shows gaps because no energy is available for allocation during spawning migrations. (c) Fulton’s condition factor (black line). The shaded lines represent minimum and maximum condition factors attainable at that length; these increase because body mass is proportional to length to the power of 3.065. (d) Number of eggs spawned (in millions). (e) Food availability in the stochastic environment measured relative to the mean. (f) Probability of survival until age (note the logarithmic y axis).

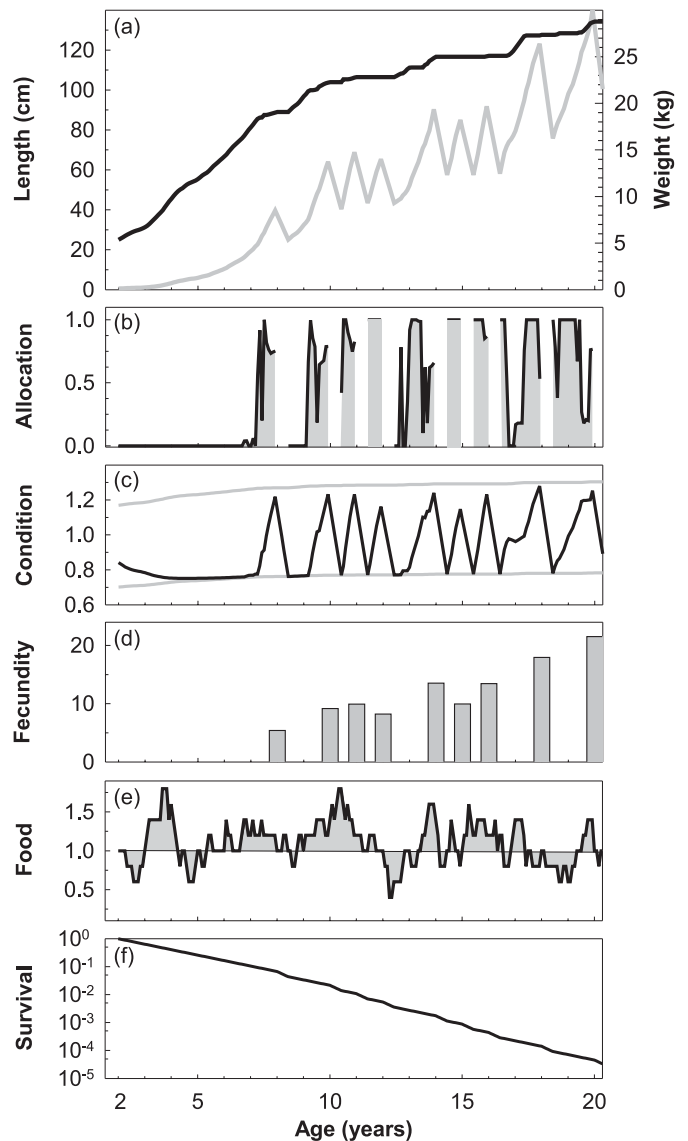
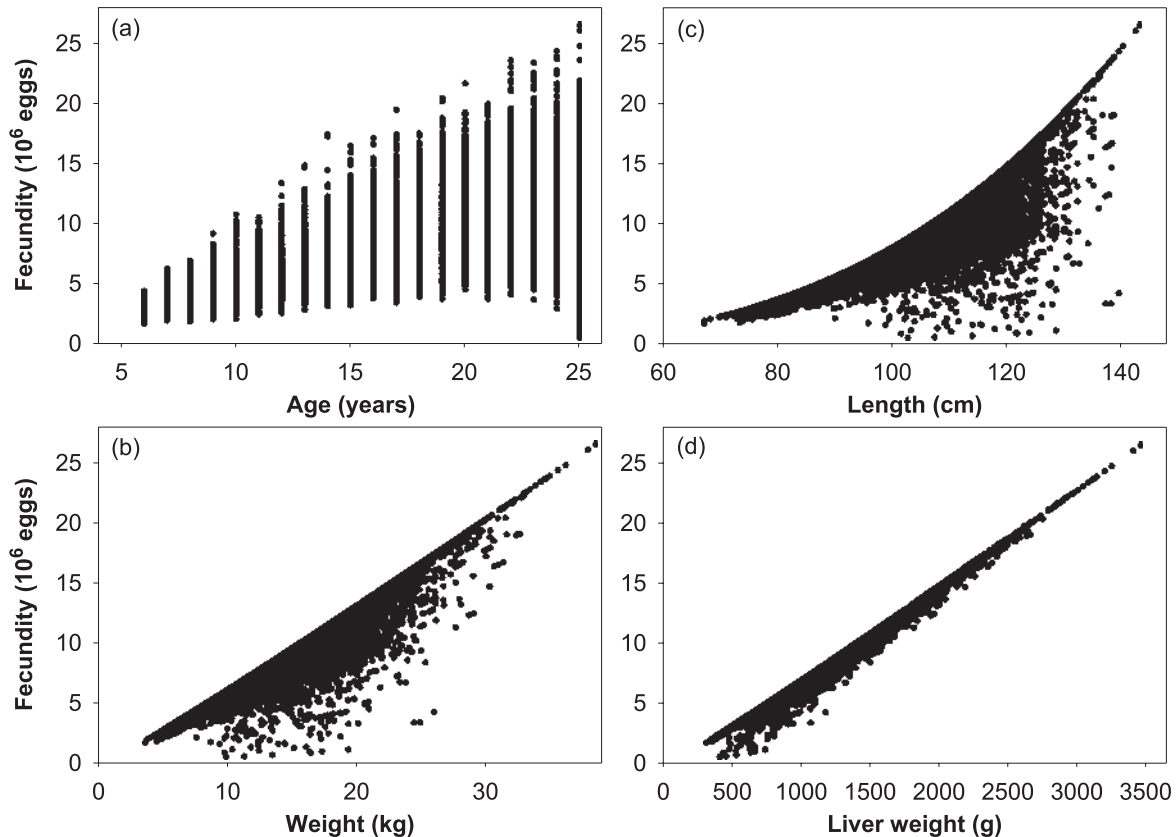


Fig. 5. Fecundity in relation to various individual characteristics. The y axis is common for all graphs and shows fecundity in millions of eggs. The results are from population simulation in a stochastic environment for 1000 years. (a) Fecundity vs. age (years). (b) Fecundity vs. body mass (kg). (c) Fecundity vs. body length (cm). (d) Fecundity vs. liver weight (g).



allocation to stores prior to reproduction, rapid weight increase and no length growth, followed by reproduction. Curiously, this cod invested all its energy in growth also in some of the years after sexual maturation (e.g., at age 9 and partially at age 13) and skipped spawning entirely in those years. The phenomenon of skipped reproduction is studied more closely in Jørgensen et al. (2006). Food availability (Fig. 4e) also influenced growth and reproduction. The variable food availability that this cod experienced while immature lead to concomitant variations in growth rate (visible in Fig. 4a). Poor food availability also coincided with skipped spawning at age 13 and age 19. Survival probability until a given age dropped faster when at the spawning grounds as the combined mortality from fishing and reproduction is higher than the fishing mortality at the feeding grounds (Fig. 4f; note the logarithmic axis).

Fecundity will vary with the individual's size, its stored energy, and the size-dependent energetic cost of migration. Some relations with fecundity are shown to visualise these effects (Fig. 5). Maximum and average fecundity were increasing with age, but older individuals were also showing a higher variance (Fig. 5a). This occurs for two reasons. First, a higher age will reduce the importance of growth per se and will tend to favour reproduction. Because of the terminal age in the model, the expected future lifespan is lower at higher ages. This reduces the value of the future component of reproduction relative to the present, meaning that energy would best be used for reproduction. In economic terms, reproduction is low-risk instantaneous liquidation of available

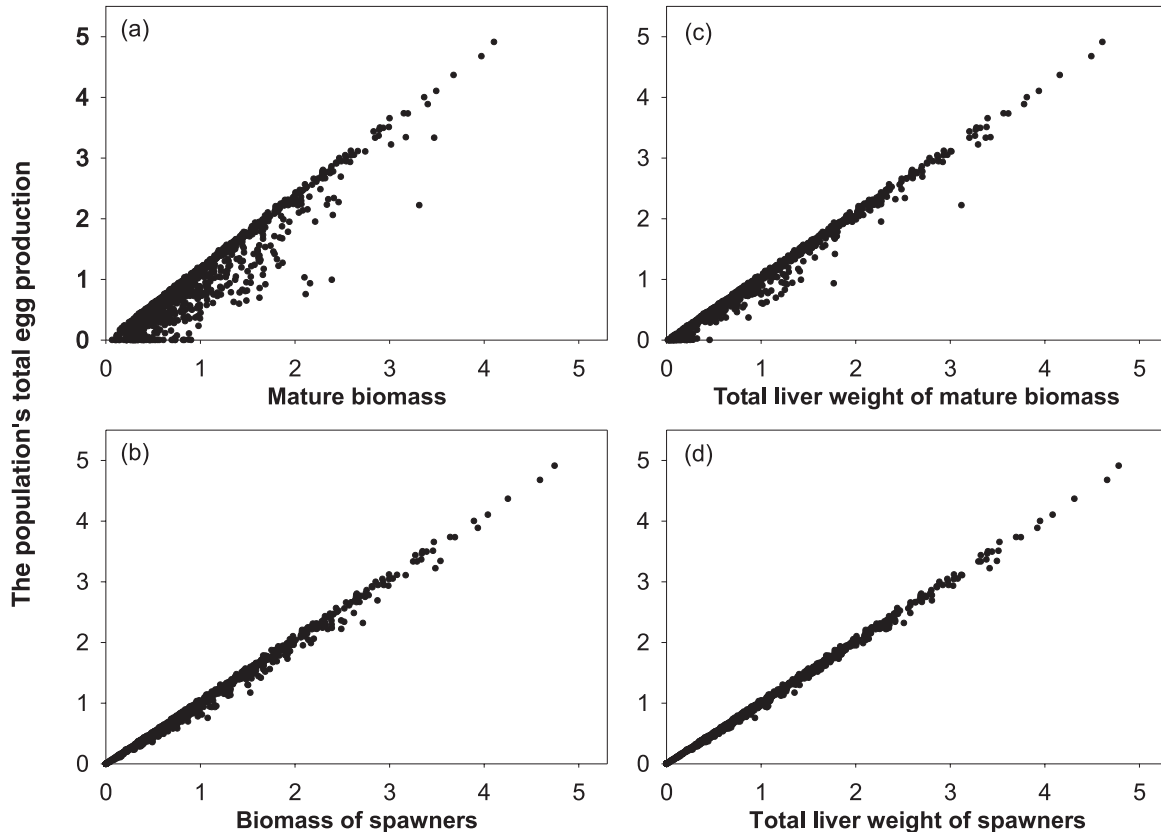
capital (stored energy), whereas growth is an investment in the future, subjected to a payoff that is becoming increasingly more risky with higher age (or, in terms of the strategy, the devaluation rate is increasing with senescence). Second, older individuals are usually larger and will thus spend relatively less energy for the migration. This gives them more leeway than smaller fish, and although small fish were forced to have full energy stores to spawn, spawning fish of larger size would show higher variance in their stored energy.

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

Stock and recruitment

The picture looked somewhat different for egg production at the population level (Fig. 6), as variation at the indi-

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



vidual level may cancel out or become amplified by correlations between individual states in the population. Variance was highest when plotted against total biomass of all sexually mature individuals (coefficient of variation for linear regression $r^2 = 0.897$; Fig. 6a). Removing sexually mature individuals that did not engage in spawning removed a lot of the variance (Fig. 6b; $r^2 = 0.995$). Liver weight was an even better predictor of egg production at the population level compared with its predictive ability for individual cod (Fig. 6c; $r^2 = 0.986$). When the population's total egg production was plotted against total liver weight of only the individuals that were actually spawning, the points fell more or less onto a straight line (Fig. 6d; $r^2 = 0.998$).

Maturity and fecundity relationships were also influenced by past food availability (Fig. 7; all values were from January, just before the spawning migration in the simulations). As predictor of mature biomass (defined as all fish that spawned for the first time this year or had spawned previously), the tightest relationship was obtained by averaging food availability over the last two years (Fig. 7a). For the stock's total egg production, the best relationship was obtained when mean food availability was averaged over the last year (Fig. 7b). The difference in time scales between these two relationships reflect that building gonads is a

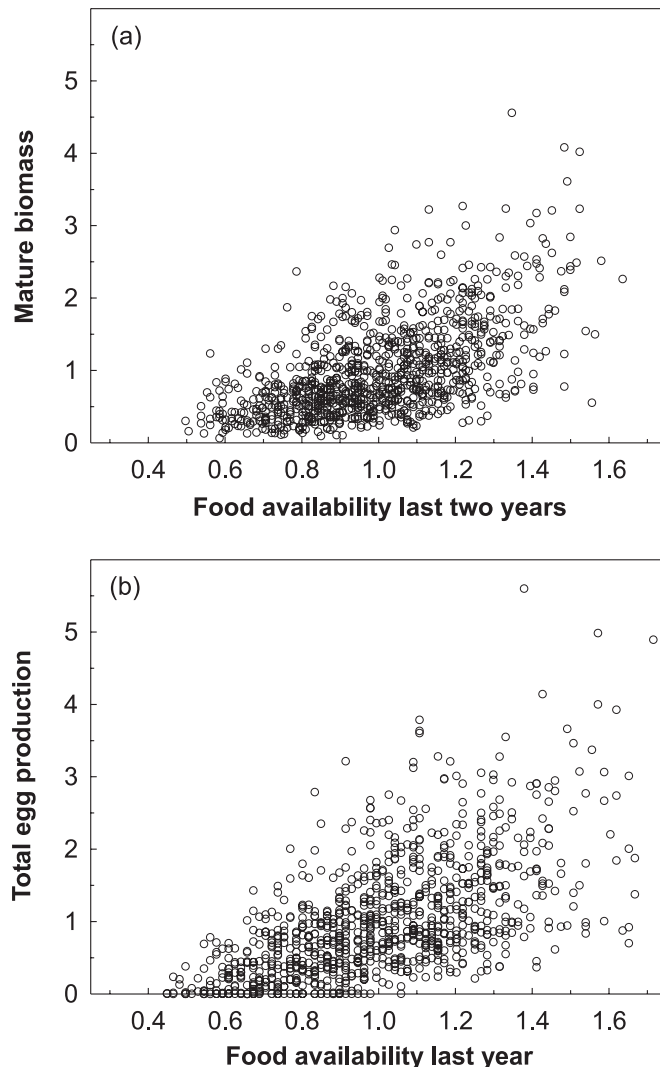
faster process than increasing mature biomass, which relies on both maturation and growth.

Discussion

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

We make three assumptions: (i) energy can only be used once; (ii) energy allocation is optimal at every point in life in the sense that it maximises fitness; and (iii) the fitness of an individual is approximated by its expected future reproductive value (true when density dependence acts early in life and the population is in equilibrium (Mylius and Diekmann 1995)). This model makes predictions about life histories from first principles by finding optimal phenotypes. When compared with data, a fit between the predicted life histories and those realised in nature makes it likely that the most important assumptions are built into the optimality

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



model and that the model turn can be used to formulate or test hypotheses under a variety of ecological conditions (Sutherland 2005). The model provides a level of detail and realism that can readily be compared with field and experimental data, and the fit in terms of both growth and maturation is promising for further comparisons with field observations.

Abstract versus complex models

Models with many parameters, such as the one presented here, are sometimes accused of being overly complex.

Models can be complex in many ways, however. Although our model is rich in mathematical and mechanistic detail, it has a low level of abstraction. Abstract assumptions are replaced by a detailed and realistic formulation of energy allocation. We have aimed at parameters with sound biological meaning and included extensive arguments for the choice of parameter values. Species- and stock-specific parameters are required to make predictions about real-world scenarios. The results presented here are quite robust, as the patterns and results reported in this paper and in Jørgensen et al. (2006) are consistent throughout a wide range of parameter combinations.

Some of the properties of this model that resemble real-world dynamics, such as indeterminate growth, variation in age and size at maturation, and skipped spawning, do not occur if we switch off, for instance, the temporal variability in food intake. In a life history model for the Müller's pearlside (*Maurolicus muelleri*), stochasticity in the environment also lead to bet-hedging strategies and a 2-year life cycle instead of reproduction within 1 year only (Strand et al. 2002). Environmental variability is inherent in biological systems, and the observation that several real-world phenomena only occur when sufficient stochasticity is part of a model suggests that they are adaptations to a variable environment. Furthermore, these adaptations affect population dynamics and ecological interactions. This basic insight is an argument for including stochasticity in models, especially where adaptations are concerned. Much of the rest of the complexity in this model is built around this stochasticity: size has to be included as a state because the variable environment will lead to temporal variations in size-at-age, and storing energy is a means of buffering environmental variation.

Life history optimisation models

This model aptly recaptures complex life history phenomena. Optimisation models have traditionally predicted determinate growth, where allocation should shift abruptly from growth to reproduction at a fixed point in life (e.g., Taborsky et al. 2003). The gradually increasing allocation to reproduction, as seen in the decelerating growth for individuals in our model, is common in nature but only rarely reproducible in models (but see Kozłowski and Teriokhin (1999); indeterminate growth is reviewed by Heino and Kaitala (1996)). Our model also shows that cod may skip reproduction in some years, and this phenomenon of skipped reproduction has, to our knowledge, not previously been reproduced in models (Jørgensen et al. 2006). Growth in the model also fits well with observed growth patterns in terms of both length- and weight-at-age when representative parameter values are used. In summation, we feel confident that the model behaves well and predicts reasonable and realistic growth and maturation patterns, and therefore, the results increase our understanding of the evolution of life history strategies in fish.

In principle, the model (as is typical for dynamic programming models) does not separate between phenotypic plasticity and evolutionary change — it simply finds the optimal life history strategies for a given set of parameters. The reaction norm concept describes the interaction between gene and environment and is relevant for maturation pro-

cesses as a fixed, genetically determined reaction norm can cause maturation to occur over a range of sizes and ages as the environment changes (Stearns and Koella 1986). The concept has been extended to the probabilistic maturation reaction norm as a method to analyse maturation data (Heino et al. 2002). The rationale behind the reaction norm approach is that size-at-age, which naturally reflects past growth rate, should mean more for the timing of sexual maturation than size or age alone. Because age and length are states, our model includes the phenotypic plasticity described by the maturation reaction norm concept and also uses stored energy as an additional dimension to fine-tune maturation dynamics.

Stock and recruitment

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

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

In nature, similar trade-offs determine the maximum fecundity (i.e., the upper limit). For example, how does a bulging belly influence swimming efficiency or feeding (is there room for digestion)? Will large gonads impair the functionality of the swim bladder (Ona 1990)? If so, what are the potential consequences? To what degree will activity level at the spawning grounds influence reproductive success? These trade-offs are harder to model because we know less about them.

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

to reduce the variance when egg production is plotted as a function of population-level characteristics.

At the individual level, liver weight was the best proxy, and this proxy also performed well at the population level. However, excluding the nonspawning part of the population provided even better predictions than using the total liver weight of the mature population. Skipped spawners will contribute to the stock's total liver weight without producing any eggs and will therefore be the source of much of the variation. This goes for both the mature biomass – egg production relationship, as well as the relationship between total liver weight and egg production. The phenomenon of skipped spawning is studied in greater detail in Jørgensen et al. (2006), providing an example application of this model to more complex questions of ecology and life history.

The influence of density dependence

With the optimisation technique used in this paper, dynamic programming, it is not straightforward to find optimal life history strategies when a population is regulated by density dependence (Houston and McNamara 1999; Clark and Mangel 2000). The model can be turned into a dynamic game, but this would require a much more complex model (McNamara et al. 1997). Simulations of population dynamics, however, require that some regulatory mechanism controls population abundance, otherwise the population would go extinct or grow exponentially and infinitely. As a consequence, life history allocation strategies are found by optimisation without density dependence in this model, and the strategy is thereafter simulated in a population where density dependence acts on juvenile survival. The fit between the model's predictions and field data suggests that the model recaptures much of the ecological realism for this stock, even without adaptation to density dependence.

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

In conclusion, there is a promising agreement between field data and the model prediction of growth and maturation. In addition, the model gives a very realistic appearance of reproduction and other ecological interactions. Modelling

tools such as this one can therefore be used for large-scale experiments that are logistically impossible or awkward in the field or lab. Because the entire population, structured by age, size, and stored energy, is available throughout the stochastic simulation of population dynamics, a large array of various data can be explored in a more experiment-like way (Peck 2004). For instance, the model can be used to study effects of increased fishery mortalities: is the increasing mortality imposed by fisheries sufficient to induce life history evolution (e.g., Law and Grey 1989; Heino 1998; Olsen et al. 2004)? Another example, to which this model has already been applied, is skipped reproduction in fish (Jørgensen et al. 2006). The life history model suggests that the counterintuitive phenomenon of skipped spawning may be more common than previously believed and gives us the opportunity to study the underlying logic. The model provides a tool for large-scale investigations of the life history of cod in different ecological settings. Life history models, such as the one presented here, are powerful tools for investigating driving forces behind instantiated life history strategies, as well as assessing and predicting potential changes derived from altered external forcing such as fisheries and climate change.

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Appendix A. Justification for choice of minimum and maximum condition factors.

Growth in the model was sensitive to the choice of minimum and maximum condition factors. The following reasons for choosing K_{\min} and K_{\max} were therefore tightly coupled with sensitivity tests and comparisons with growth data. In an experiment following individual cod throughout the spawning season (length 56–87 cm; only females considered here), mean prespawning condition factor was 1.39 (range 1.19–1.75), while the average for spent cod was 0.97 (range 0.81–1.13) (Fordham and Trippel 1999). Using these condition factors for K_{\min} and K_{\max} in the model, however, gives higher condition factors and weight-at-age than are observed for the Northeast Arctic cod stock. This may be partly because eggs swell prior to spawning by taking up water (Tyler and Sumpter 1996; Fordham and Trippel 1999), which may artificially inflate condition factors for prespawning cod so that they no longer reflect the true size of energy stores. The extent of water uptake can be illustrated by the fact that total volume of eggs spawned was on average 150% of post-spawning body volume in the same study (Fordham and Trippel 1999). Also, cod were fed ad libitum throughout the spawning period in that study, and the easy access to food compared with natural conditions may have improved final condition. A somewhat lower maximum value, $K_{\max} = 1.25$, was therefore selected. In a starvation experiment, cod died when condition factors reached 0.44 (range 0.36–0.56; length 31–55 cm), although liver energy stores were depleted before this (Dutil and Lambert 2000). The K_{\min} in this model should, however, reflect the condition at which routine energy stores are depleted, not the level to which severe food stress can atrophy muscle mass before death occurs. A value of $K_{\min} = 0.75$ was therefore chosen through thorough testing as it reproduced appropriate weight-at-length compared with field data (e.g., Fig. 4). Condition factors in the model are given relative to a standard length $L_{\text{std}} = 70$ cm, which means that realised K_{\min} is in the range 0.71–0.74 for the lengths used in Dutil and Lambert (2000).

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