

Simple energy-budget model for yolk-feeding stages of Atlantic cod (*Gadus morhua*)

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ABSTRACT

Atlantic cod (*Gadus morhua*) is a commercially important species, and therefore, understanding the influence of environmental factors and anthropogenic stressors on its early life stages is of considerable relevance. In this contribution, we apply a simple and generic energy-budget framework (DEBkiss) to data for the yolk-feeding stages of cod. The model is capable of explaining the changes in yolk volume, dry weight, oxygen use and body length, simultaneously with a small number of parameters. The calibrated model was subsequently successfully tested with other data sets. Interestingly, the light conditions after hatching affect growth and respiration rates, which is traced to a change in the maintenance costs (linked to swimming activity). Despite the satisfactory performance of the model, several uncertainties remain. Especially the bioenergetics around the point of complete yolk absorption require further attention, which is complicated by the fact that the behaviour around this point differed between data sets. The presented model can be used for exploring effects of stressors on early-life stages of cod, and likely for other aquatic egg-laying species as well.

1. Introduction

Atlantic cod (*Gadus morhua*) is a fish species of substantial economic importance, and therefore there is considerable interest in the effects of environmental factors and stressors (such as temperature and xenobiotics) on its life history. The early-life stages of fish are crucial for recruitment of both natural and cultured fish stocks (Kamler, 2008), and are regularly specifically sensitive to chemical stress (see e.g., Petersen and Kristensen, 1998; Massei et al., 2015). Interpreting, understanding and ultimately predicting stressor effects on the life history requires bioenergetic models (Jager et al., 2013). In all animals, food is used to fuel the energy-demanding processes of maintenance, activity, growth, development and reproduction. In doing so, the individual needs to obey the conservation laws for mass and energy, which helps to structure the modelling efforts.

The yolk-feeding stages are of particular interest from a bioenergetic viewpoint as most of them can be considered as semi-closed systems (Heming and Buddington, 1988): practically all of the energy that the developing embryo uses for its development is locked inside the egg in the form of endogenous yolk. This makes them ideal objects to study the effects of environmental factors and stresses on their energy budget. Specific bioenergetic models have been proposed for fish development

over the yolk-feeding stages (Beer and Anderson, 1997; Jaworski and Kamler, 2002), but we aim for a more general treatment, embedding the yolk stages into the rest of the life cycle and linking fish to other animal species. Dynamic Energy Budget (DEB) theory (Jusup et al., 2017; Sousa et al., 2010) offers such a generic and inclusive bioenergetics representation, covering the entire life cycle (from egg to death) for all forms of life. The DEBkiss framework (Jager et al., 2013; Jager, 2016) is derived from DEB theory by applying several simplifications to ease parameterisation, interpretation and practical applications, such as in interpreting the effects of chemical stress (Barsi et al., 2014) and ocean acidification (Jager et al., 2016).

The most prominent simplification in DEBkiss is the removal of ‘reserve’ as a state variable in the model. For many applications, this turns out to be an acceptable simplification (see list of papers at http://www.debtox.info/debkiss_appl.html). The result is a simple model for bioenergetics of (ectothermic) animals over their entire life cycle, including the embryonic stages (Jager et al., 2013; Barsi et al., 2014). However, for eggs, the removal of reserve required some additional thought. DEB theory considers the yolk as part of the reserve, and clearly, no model for embryo bioenergetics can work without a state variable that considers yolk. In DEBkiss, yolk is treated as a buffer, handed over by the mother to the egg, which is assimilated, in a similar

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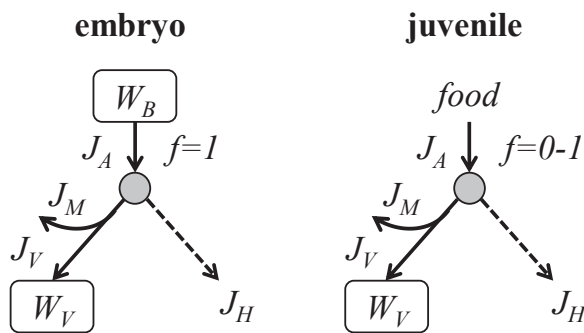


Fig. 1. Schematic representation of the DEBkiss model for embryos and juveniles; in a DEB context, the transition from embryo to juvenile is defined by the start of (the ability for) external feeding. State variables are egg buffer or yolk (W_B) and structure (W_V), and fluxes are for assimilation (J_A), maintenance (J_M), growth (J_V) and maturation (J_H). The scaled functional response f is 1 for embryos (*ad libitum*) and depends on food availability for juveniles (zero when no food is present). Grey circle is a split of the assimilation flux, with a fraction of κ allocated to maintenance and growth.

fashion as assimilation of food by the free-swimming feeding stages. This assumption is quite similar to the assumptions made for yolk absorption by Beer and Anderson (1997) and Jaworski and Kamler (2002).

To test the performance of the simple DEBkiss model for egg development and yolk feeding, we apply it to data for the Atlantic cod. Once parameterised and tested, this model may prove to be useful to interpret and predict the effects of environmental changes and stressor effects on the yolk-feeding stages of cod. As the DEBkiss model is generic, it can then likely be applied to other fish species (and even other egg-laying animals) as well.

2. Methods

2.1. Basic model for embryos

A detailed description of DEBkiss can be found elsewhere (Jager et al., 2013; Jager, 2016); below a summary is given as far as relevant for the early life stages (reproduction is excluded from the model description here). The model structure for these stages is schematically shown in Fig. 1, and all symbols used in this study are summarised in Table 1. Note that in DEB terminology, the embryo is the initial stage of the life cycle where the animal does not feed exogeneously, and the juvenile stage starts with the ability to feed exogeneously. The points of hatching and metamorphosis (the end of the larval stage) are not stage switches from an energetic viewpoint.

Over its early development, the embryo goes through a series of events, for cod described in detail by Hall et al. (2004). These events represent major changes in morphology of the embryo, but for our DEBkiss model, all this detail will be ignored. The egg is treated as consisting of two state variables: the mass of the egg buffer W_B (representing the yolk) and the mass of structure W_V (representing the embryo or larvae without the yolk sac). The egg buffer is assimilated at a rate J_A , and structural mass increases with a growth flux J_V :

$$\frac{d}{dt}W_B = -J_A \quad \text{until } W_B = 0, \quad \text{with } W_B(0) = W_{B0} \quad (1)$$

$$\frac{d}{dt}W_V = J_V \quad \text{with } W_V(0) = W_{V0} \quad (2)$$

To facilitate the links between mass, surface area, and body length, it is practical to work with volumetric length (L), which is the cubic root of structural volume (using the dry-weight density d_V). Volumetric length can in turn be linked to more practical length measures (L_w , e.g., standard length, SL, in fish) by a shape-correction coefficient (δ_M):

Table 1

Explanation of symbols used in this study. For parameters and constants, values are given, which are either fitted (see Fig. 2; 95% confidence interval in parentheses) or fixed (n.e., not estimated). Values for the yield coefficients are taken from Jager et al. (2013); other fixed values explained in the text. When yolk is present $f = 1$, and otherwise $f = 0$. Rate constants represent a temperature of 6 °C.

Sym.	Explanation	Value (C.I.)	Unit
<i>Primary parameters</i>			
f	Scaled functional response	1/0 (n.e.)	–
J_{Am}^a	Maximum area-specific assimilation rate	16.0 (14.7–17.1) 10^{-3}	$\text{mg mm}^{-2} \text{d}^{-1}$
J_V^v	Volume-specific maintenance costs	4.37 (3.87–5.02) 10^{-3}	$\text{mg mm}^{-3} \text{d}^{-1}$
y_{AV}	Yield assimilates on structure (shrinking)	0.8 (n.e.)	mg mg^{-1}
y_{VA}	Yield structure on assimilates (growth)	0.8 (n.e.)	mg mg^{-1}
κ	Fraction of assimilation flux for soma	1 (0.949–1)	–
<i>Initial states</i>			
W_{B0}	Assimilates in freshly-laid egg	100 (96.9–104) 10^{-3}	mg
W_{V0}	Structure in freshly-laid egg	2.35 (1.48–3.64) 10^{-3}	mg
<i>Conversions</i>			
d_B	Dry-weight density of egg buffer	0.0745 (0.0714–0.0796)	mg mm^{-3}
d_C	Carbon content of yolk and structure	0.40 (n.e.)	mg mg^{-1}
d_V	Dry-weight density of structure	0.15 (n.e.)	mg mm^{-3}
F_{RQ}	Respiratory quotient	0.8 (n.e.)	–
W_c	Weight of chorion of egg	0.020 (n.e.)	mg
δ_M	Shape correction coefficient	0.157 (0.151–0.162)	–
<i>Fluxes and state variables</i>			
J_A	Mass flux for assimilation		mg d^{-1}
J_D	Total mass flux that is dissipated		mg d^{-1}
J_H	Mass flux for maturation/maturity maint.		mg d^{-1}
J_M	Mass flux for maintenance		mg d^{-1}
J_V	Mass flux for structure (growth/shrinking)		mg d^{-1}
J_{V0}	Overhead costs for growth/shrinking		mg d^{-1}
W_B	Mass of assimilates buffer in egg		mg
W_V	Mass of structural body		mg
<i>Derived or intermediate variables</i>			
L	Volumetric body length		mm
L_w	Physical body length (e.g., SL)		mm

$$L^3 = \frac{W_V}{d_V} \quad \text{and} \quad L_w = \frac{L}{\delta_M} \quad (3)$$

Reported water content for cod larvae (4.5–10 mm SL) is around 85% (Finn et al., 2002). This implies that we can use $d_V = 0.15 \text{ mg/mm}^3$ as a reasonable estimate for the density of structure. In our calibration data set (Finn et al., 1995), yolk is expressed as a volume, and hence we also need a dry-weight density for the egg buffer (d_B). We leave this as a free parameter to be estimated in the fit to the data, as we have no direct information on the yolk properties. Measurements on total fresh eggs (Finn et al., 1995) suggest a value close to 0.07 mg/mm^3 .

Next, we need to fill in the mass fluxes for the various processes. The assimilation flux (J_A) is proportional to a surface area of the animal, and the maintenance flux (J_M) to a volume. A fraction κ of the assimilation flux is used (with a certain efficiency, y_{VA}) for growth (J_V); the remainder (here denoted as J_H) is assumed to be dissipated. In the DEB context, the flux J_H is used for maturity and maturity maintenance; even though these processes are not explicitly followed here, specification of this flux is needed to close the mass balance and for the

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