Application of DEB theory to the life cycle of *Sardina pilchardus*

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1 Introduction

The present work aims to: (i) describe the model formulation for processes that control metabolism, reproduction and life expectancy of the sardine (*S. pilchardus*), based on the Dynamic Energy Budget (DEB) theory (Kooijman, 2000); (ii) describe a methodology for parameter estimation with Bayesian methods based on measurable quantities. The model was designed to agree with the assumptions and propositions already described in Sousa et al. (2007), and uses the most recent notation of DEB theory (Kooijman et al., 2007). The equations in the model are written so that energy and mass flow, the dynamics of state variables, and measurable quantities are expressed as functions of the basic parameters, and only they. This avoids the need for extra variables and equations, in some cases at the cost of rendering those presented not so readily interpretable.

2 Model Description

The model presented here is a basic DEB model with one reserve and one structure, whose chemical composition always reamains constant (strong homeostasis). Mass fluxes of the different elements and compounds are considered in order to ensure the conservation of

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Table 1: DEB parameters.

symbol	**units**	**description**	**process**
T_A	K	Arrhenius temperature	all
$\dot{k}_{15}$	–	reaction rate at 15°C	all
$\{\dot{b}\}$	m^3 d^{-1} m^{-2}	surface area-specific searching rate	feeding
$\{\dot{J}_{XAm}\}$	molC d^{-1} m^{-2}	surface area-specific max ingestion rate	feeding
y_{EX}	molC molC^{-1}	yield of reserve on food	assimilation
y_{VE}	molC molC^{-1}	yield of structure on reserve	growth
$\dot{v}$	m d^{-1}	energy conductance	catabolism
$\{\dot{J}_{ET}\}$	molC d^{-1} m^{-2}	surface area-specific maintenance	heating
$[\dot{J}_{EM}]$	molC d^{-1} m^{-3}	volume-specific somatic maintenance	maintenance
$\dot{k}_J$	d^{-1}	volume-specific maturity maintenance	maintenance
κ	–	allocation fraction	catabolism
E_H^b	ε	threshold of energy investment at birth	maturation
E_H^p	ε	threshold of energy investment at puberty	maturation
κ_R	–	reproduction efficiency	reproduction
$[M_R^s]$	molC m^{-3}	volume-specific egg/sperm batch mass	reproduction
a	m$^3\varepsilon^{-1}$ d^{-1}	endogenous damage constant	mortality
b	m^3	predation-related constant	mortality
c	-	fisheries catchability constant	mortality
d	-	fisheries selectivity intercept	mortality
e	m^{-3}	fisheries selectivity slope	mortality

mass. Ammonia, water and carbon dioxide are assumed as the mineral excretions, and faeces are assumed as the only product of the organism. The conservation of energy is also ensured.

An organism is described by means of four state variables: reserve energy (E), structural volume (V), reserve energy invested into maturation (E_H) and egg/sperm mass (M_R). We assume that growth is isomorphic.

2.1 Energy flow [ε d^{-1}]

- Feeding

$$\dot{p}_X = \frac{\{\dot{J}_{XAm}\}V^{2/3}\mu_X}{1 + \frac{\{\dot{J}_{XAm}\}}{X\{\dot{b}\}}}$$

- Assimilation

$$\dot{p}_A = \frac{\dot{p}_X y_{EX} \mu_E}{\mu_X}$$

- Structure maintenance

$$\dot{p}_M = [\dot{J}_{EM}]\mu_E V$$

Table 2: Chemical indices.

symbol	**units**	**description**	**Element**
n_{NX}	molN molC^{-1}	chemical index of nitrogen in food	*nitrogen*
n_{NV}	molN molC^{-1}	chemical index of nitrogen in structure	*nitrogen*
n_{NE}	molN molC^{-1}	chemical index of nitrogen in reserve	*nitrogen*
n_{NP}	molN molC^{-1}	chemical index of nitrogen in product	*nitrogen*
n_{HX}	molH molC^{-1}	chemical index of hydrogen in food	*hydrogen*
n_{HV}	molH molC^{-1}	chemical index of hydrogen in structure	*hydrogen*
n_{HE}	molH molC^{-1}	chemical index of hydrogen in reserve	*hydrogen*
n_{HP}	molH molC^{-1}	chemical index of hydrogen in product	*hydrogen*
n_{OX}	molO molC^{-1}	chemical index of oxygen in food	*oxygen*
n_{OV}	molO molC^{-1}	chemical index of oxygen in structure	*oxygen*
n_{OE}	molO molC^{-1}	chemical index of oxygen in reserve	*oxygen*
n_{OP}	molO molC^{-1}	chemical index of oxygen in product	*oxygen*

Table 3: Other model parameters.

symbol	**units**	**description**
δ_M	m m^{-1}	shape coefficient
μ_E	ε molC^{-1}	chemical potential of reserve
μ_X	ε molC^{-1}	chemical potential of food
$[M_V]$	molC m^{-3}	density of structure

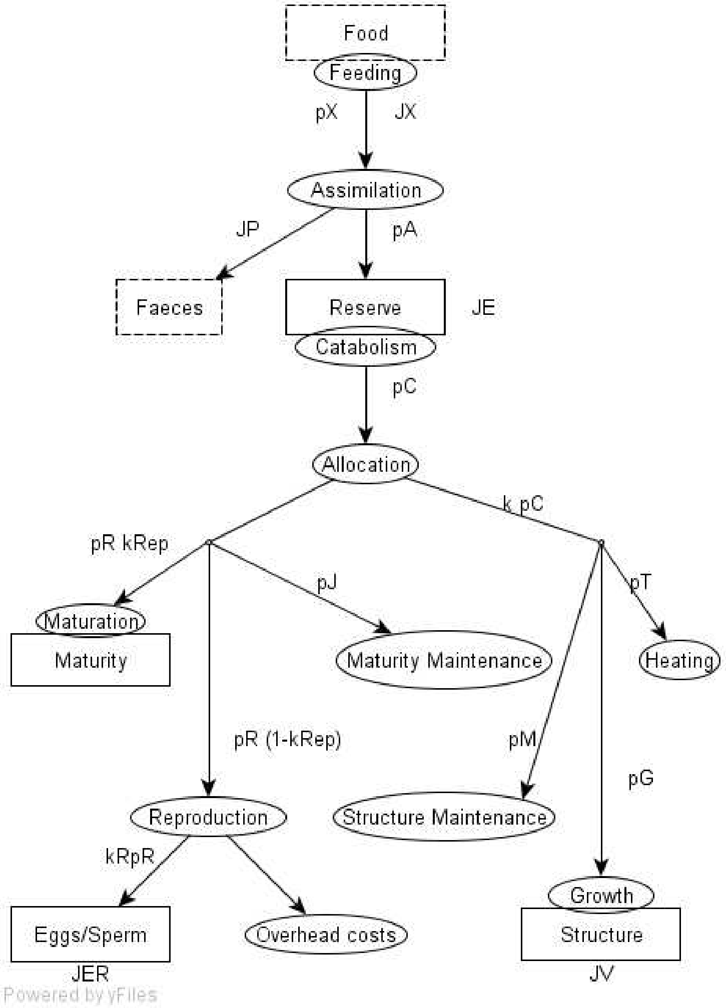

Figure 1: Energy fluxes ($\dot{p}_*$), mass fluxes ($\dot{J}_*$), processes (ellipses), sources and sinks (dashed rectangles) and state variables (solid rectangles) in the DEB model.

- Heating

$$\dot{p}_T = \{\dot{J}_{ET}\}\mu_E V^{2/3}$$

- Catabolism

$$\dot{p}_C = \frac{\dot{v}V^{2/3} + \frac{y_{VE}}{\mu_E[M_V]}(\dot{p}_M + \dot{p}_T)}{\frac{V}{E} + \frac{\kappa y_{VE}}{\mu_E[M_V]}}$$

- Growth

$$\dot{p}_G = \kappa \dot{p}_C - \dot{p}_M - \dot{p}_T$$

- Maturity maintenance

$$\dot{p}_J = \dot{k}_J E_H$$

- Maturation and reproduction

$$\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$$

2.2 Fluxes of Compounds and Mass Balance

The general equation that ensures mass conservation is

$$\mathbf{0} = \boldsymbol{n}_{Min}\dot{\boldsymbol{J}}_{Min} + \boldsymbol{n}_{Org}\dot{\boldsymbol{J}}_{Org}$$

where $\dot{\boldsymbol{J}}_{Min}$[mol d^{-1}] is the vector with the molar fluxes of the mineral compounds (carbon dioxide $\dot{J}_{CO_2}$, water $\dot{J}_{H_2O}$, dioxygen $\dot{J}_{O_2}$, nitrogenous waste $\dot{J}_{N_{waste}}$); $\boldsymbol{n}_{Min}$[mol molC^{-1}] and $\boldsymbol{n}_{Org}$[mol molC^{-1}] represent the chemical indices of the mineral and organic compounds, respectively; $\dot{\boldsymbol{J}}_{Org}$ is the vector with the molar fluxes of the organic compounds (food $\dot{J}_X$, structure $\dot{J}_V$, reserve $\dot{J}_E + \dot{J}_{E_R}$, and product $\dot{J}_P$). The assumptions are: (i)$\dot{J}_{N_{waste}}$ represents ammonia excretions: $\dot{J}_{N_{waste}} \equiv \dot{J}_{NH_3}$; (ii) product is interpreted as faeces, and faeces production is coupled to food intake only.

2.2.1 Mass Flow of Organic Compounds [molC d^{-1}]

- Food

$$\dot{J}_X = \frac{\dot{p}_X}{\mu_X}$$

- Structure

$$\dot{J}_V = \frac{\dot{p}_G y_{VE}}{\mu_E}$$

- Reserve

$$\dot{J}_E = \frac{\dot{p}_A - \dot{p}_C}{\mu_E}$$

- Eggs/Sperm

$$\dot{J}_{E_R} = (1 - k_{Rep})\,\frac{\dot{p}_R \kappa_R}{\mu_E}$$

where

$$k_{Rep} = \begin{cases} 1, & \text{if } E_H < E_H^P \\ 0, & \text{otherwise} \end{cases}$$

- Products

$$\dot{J}_P = \frac{\dot{p}_A - \dot{p}_X}{\mu_P}$$

2.2.2 Mass Flow of Mineral Compounds [mol d^{-1}]

- Ammonia

$$\dot{J}_{NH_3} = -\left(n_{NX}\dot{J}_X - n_{NV}\dot{J}_V - n_{NE}\left(\dot{J}_E + \dot{J}_{E_R}\right) + n_{NP}\dot{J}_P\right)$$

- Water

$$\dot{J}_{H_2O} = -\frac{1}{2}\left(n_{HX}\dot{J}_X - n_{HV}\dot{J}_V - n_{HE}\left(\dot{J}_E + \dot{J}_{E_R}\right) + n_{HP}\dot{J}_P + 3\dot{J}_{NH_3}\right)$$

- Carbon dioxide

$$\dot{J}_{CO_2} = -\left(\dot{J}_X - \dot{J}_V - \left(\dot{J}_E + \dot{J}_{E_R}\right) + \dot{J}_P\right)$$

- Dioxygen

$$\dot{J}_{O_2} = -\frac{1}{2}\left(n_{OX}\dot{J}_X - n_{OV}\dot{J}_V - n_{OE}\left(\dot{J}_E + \dot{J}_{E_R}\right) + n_{OP}\dot{J}_P + \dot{J}_{H_2O} + 2\dot{J}_{CO_2}\right)$$

2.3 Dynamics of state variables

- Structure, $V[\mathrm{m}^3]$

$$\frac{dV}{dt} = \frac{\dot{J}_V}{[M_V]}$$
$$V^o = 0$$

- Reserve, $E[\varepsilon]$

$$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$$

$$E^o = \mu_E \left\{ \delta_M \left(\frac{\mu_E x(1-\kappa)}{E_H^b} \right)^{\frac{1}{3}} - \frac{B_x(4/3,0)[\dot{J}_{EM}]\kappa^{\frac{1}{3}}}{3\dot{v}} \left(\frac{y_{VE}}{[M_V]} \right)^{\frac{4}{3}} \right\}^{-3}$$

where

$$x^{-1} = 1 + \frac{\dot{p}_A y_{VE} \kappa}{\mu_E [M_V] V^{2/3} \dot{v}}$$

- Maturity, $E_H[\varepsilon]$

$$\frac{dE_H}{dt} = \begin{cases} \dot{p}_R, \text{ if } E_H < E_H^p \\ 0, \text{ otherwise} \end{cases}$$
$$E_H^o = 0$$

- Eggs/Sperm, $M_R[\mathrm{molC}]$

$$M_R = \begin{cases} 0, \text{ if } E_H < E_H^p \\ \frac{\kappa_R}{\mu_E} \int_{t^\star}^{t} \dot{p}_R(t)\, dt, \text{ otherwise} \end{cases}$$

The initial value of $t^\star$ is the time when maturity was reached. If $M_R = V[M_R^s]$, then the organism spawns and $t^\star \equiv t$. This approach assumes an unique spawning event that empties the reproduction buffer.

2.4 Mortality

- Probability of surviving endogenous damage

$$P_E(t) = \exp\left\{ -a \int_{t_b}^{t} \left[\frac{1}{V(t_1)} \int_{t_b}^{t_1} \left(\int_{t_b}^{t_2} \dot{p}_C(t_3) dt_3 \right) dt_2 \right] dt_1 \right\}$$

t_b represents time at birth, t the current time and $P_E(t)$ the probability of being alive in the interval $[t_b, t]$, considering endogenous damage

- Probability of surviving starvation

$$P_S(t) = \begin{cases} 1, \text{ if } E > 0 \\ 0, \text{ otherwise} \end{cases}$$

- Probability of surviving predation

$$P_P(t) = \exp\left(-\frac{b}{V}\right)$$

- Probability of retention in fishing gear

$$P_F(t) = \frac{c}{1 + \exp\left(d + eV\right)}$$

- General survival probability

$$P[t_\dagger > t] = P_E(t)P_S(t)P_P(t)(1 - P_F(t))$$

3 Parameter estimation with Bayesian methods

The DEB parameters listed above are species-specific and their values are unknown. Instead of the traditional approach to DEB parameter estimation (van der Meer, 2006; Sousa et al., 2006; Kooijman et al., 2007), we use the Bayesian method described in the next paragraphs.

The goal is to find a distribution for each parameter such that the mean is a compromise solution between the one provided by prior information and the one that maximizes the likelihood associated with experiments and measurments performed on specimens of our species of interest. Since in many cases this posterior distribution cannot be found in closed form, we use Markov chain Monte Carlo (MCMC) methods to explore it. Thus we steer away from assuming that the vector of parameters follows a multivariate Normal distribution. This brings large benefits when analyzing correlations between parameters and when constructing adequate credibility intervals for them.

3.1 Prior distributions

Basing on both theory and data available for similar species, we start by defining a suitable probability distribution for our species' parameters. As the Normal and the

Gamma distibutions are good candidates, this requires us to define the mean and the variance for each parameter. The mean can be given by a weighted average of the parameters for similar species, where the weights reflect the degree of proximity. The variance can be given by weighting the estimated parameter variances for the similar species, or be inversely proportional to the richness of information we have beforehand: number of similar species, proximity to the most similar species, etc.. The best method to define the prior mean and variance - as well as the distibution itself - is a hot subject in Bayesian statistics. We point out, however, that if our species is well-studied these choices have little influence on the final results.

3.2 Posterior distributions

A significant amount of published work can be used to provide information about our parameters. This happens because many experiments yield measurable quantities that are linked to the DEB parameters, through the equations listed in section 4. The process of combining the prior with the likelihood generally does not yield a distribution in closed form (i.e., it is no longer Normal or Gamma). Thus, to learn about the parameters' posterior distribution, we use an overrelaxed slice sampler (Neal, 2003) and a MCMC method. We switch to a regular slice sampler every ten iterations of the MCMC. The approach is analogous for all parameters, so we let y denote a general parameter. We also denote y^n as a newly sampled value of y and y^p as a value sampled in the previous iteration of the MCMC. The following paragraph summarizes the rationale and algorithm of the slice sampling approach.

In both slice samplers, a slice of the distribution is defined, where the density is always greater than a threshold given by a random fraction (between 0 and 1) of the density at y^p. In the regular sampler y^n is sampled independently from y^p. In the overrelaxed sampler, the full conditional distribution is assumed to have just one mode, and y^n is chosen so that y^p and y^n are on opposite sides of the mode. This approach accelerates convergence to the posterior distribution. We follow the scheme of Neal (2003) to define the initial slice, trim its edges and obtain y^n. The initial slice is set to have a width of 20% the standard deviation of the prior distribution, and is randomly placed in the parameter's domain (usually $\mathbb{R}^+$), provided that it includes y^p. A random variate with standard uniform distribution is drawn and multiplied to the likelihood of y to obtain the threshold. With an iterative procedure, the limits of the initial slice are extended or contracted so that the posterior at its edges remains bigger than the threshold. Once the lower (L) and the upper (U) edges of final slice are defined, the overrelaxed slice sampler chooses the new candidate according to $y^n = L + U - y^p$, while the regular slice sampler uses $y^n = L + z(U - L)$, where z is a random variate with standard uniform distribution. The candidate is accepted if its posterior exceeds the threshold. Otherwise, the overrelaxed slice sampler sets $y^n = y^p$, while the regular slice sampler redefines the slice using y^n as one of the edges and samples a new candidate. As Neal (2003) points out, for unimodal distributions the candidate is almost never rejected, as long as the edges of the slice are accurately estimated.

For convergence diagnostics, we use the methods developed by Heidelberger and Welch (1983); Gelman and Rubin (1992); Geweke (1992); Raftery and Lewis (1992b,a); Brooks and Gelman (1998), which are available in the package Bayesian Output Analysis Program `(BOA)` (Smith, 2005) within `R` (R Development Core Team, 2005). We use the default values of `BOA` to define the length of the burn-in stage, thin the chain, check stationarity and define the adequate sample size to achieve the precision required, when sampling from the posterior distribution.

4 Measurable quantities

For most of the quantities below we have already found references (papers or webpages) with available data. In these cases, we provide the respective reference in parentheses. For those that have no supporting data, we indicate what kind of information in the model would be provided, thus explaining why they are necessary.

- Food consumption, $\dot{J}_X$[molC d^{-1}], and faeces production, $\dot{J}_P$[molC d^{-1}] (this would provide information about y_{EX}, μ_E, μ_P and μ_X)

$$\dot{J}_P = \frac{\dot{J}_X}{\mu_P} \left(y_{EX} \mu_E - \mu_X \right) + \epsilon_1$$

The error term, ϵ_1, has Normal distribution with mean zero and variance σ_1^2, whose (vague) prior distribution is Gamma and posterior distribution is also Gamma. The same applies to all subsequent error terms.

- Composition of starved larvae (composition of structure)
- Composition of newly fertilized eggs (composition of reserve)
- Maximum clearance rate, $\dot{F}_{Max}$ [m^3 d^{-1}] (Garrido et al., 2007)

  $$\dot{F}_{Max} \equiv \dot{S}GO = \{\dot{b}\} \left(\delta_M L\right)^2 + \epsilon_2$$

  where $\dot{S}$[m d^{-1}] is the swimming speed, G[m^2] is the mouth gape, O[non-dimensional] is the fraction of time spent with the mouth open, and L[m] is the body length.

- Decay of prey concentration, $X(t)$[molC m^{-3}] (Garrido et al., 2007)

  $$X(t) = X(0)\exp\left(-\left(\delta_M L\right)^2 \frac{N\{\dot{J}_{XAm}\}}{X(0)V_T} t + \epsilon_3\right)$$

  where V_T[m^3] is the tank volume, L[m] is the body length of fish, and N is the number of fish. It is assumed that at the beginning of the experiment, the feeding rate per unit of surface area is equal to its maximum, $\{\dot{J}_{XAm}\}$.

- Von Bertalanffy growth coefficient, $\dot{r}_B[\varepsilon$ molC$^{-1}]$ (Fishbase: `www.fishbase.org`)

  $$\dot{r}_B = \frac{[\dot{J}_{EM}]}{\frac{3[M_V]}{y_{VE}} + \frac{3\kappa\{\dot{J}_{XAm}\}}{\dot{v}}} + \epsilon_4$$

  We assume here that food is abundant.

- Asymptotic length, L_∞[m] (Fishbase)

  $$L_\infty = \frac{\kappa\{\dot{J}_{XAm}\}y_{EX}}{\delta_M[\dot{J}_{EM}]} + \epsilon_5$$

- Number of eggs/sperm in the gonad right before spawning, B [$-$], and the body mass after the gonad has been surgically removed, M_{-R}[molC] (Ganias et al., 2004)

  $$B = \frac{[M_R^s]V\mu_E}{E^o} + \epsilon_6$$

  Again we assume that food is abundant and hence

  $$x^{-1} = 1 + \frac{\{\dot{J}_{XAm}\}y_{EX}y_{VE}\kappa}{[M_V]\dot{v}},$$

which simplifies the computation of E^o, and

$$M_{-R} = [M_V]V + \frac{E}{\mu_E} = V\left([M_V] + \frac{\{\dot{J}_{XAm}\}}{\dot{v}}\right),$$

making

$$B = \frac{[M_R^s]M_{-R}\mu_E}{E^o\left([M_V] + \frac{\{\dot{J}_{XAm}\}}{\dot{v}}\right)} + \epsilon_6$$

- Length at maturity, L_p[m] (Fishbase)

$$L_p = \frac{1}{\delta_M}\left(\frac{E_H^p\kappa\{\dot{J}_{XAm}\}y_{EX}y_{VE}}{\mu_E[M_V](1-\kappa)}\right)^{\frac{1}{3}} + \epsilon_7$$

- Length at birth, L_b[m] (Fishbase)

$$L_b = \frac{1}{\delta_M}\left(\frac{E_H^b y_{VE}\kappa}{\mu_E[M_V](1-\kappa)}\right)^{\frac{1}{3}} + \epsilon_8$$

- Age at birth, a_b[d], as a function of temperature (Miranda et al., 1990)

$$a_b = \frac{3V_b^{1/3}}{\dot{v}} + \epsilon_9$$

- Longevity in the absence of food, $a_\dagger$[d] Miranda et al. (1990)

$$\int_0^{a_\dagger} \dot{p}_C(t)dt = E^o$$

  That is, in the absence of external food the embryo develops until it hatches and survives for some time more, until the reserve is completely exhausted. The time it takes for a juvenile to die depends on how much reserve the egg had to start with, and depends on the catabolic power.

- Mortality related parameters (Mendes and Borges, 2006)
  Time series data of fish landings and effort

5 Conclusions

The present work is a first approach towards modelling the population dynamics of sardine shoals off the Portuguese coast. In future work we wish to:

- implement the model in 0-D;
- couple the model to a 3-D hydrodynamic and biogeochemical model;
- write a paper.

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