

# DEB-IBM: Model Description

## Dynamic Energy Budget theory meets individual-based modelling: a generic and accessible implementation

Benjamin Martin<sup>1\*</sup>, Elke Zimmer<sup>2</sup>, Volker Grimm<sup>1</sup>, Tjalling Jager<sup>2</sup>

<sup>1</sup> Dept. of Ecological Modeling, Helmholtz Center for Environmental Research – UFZ, Permoserstrasse 15, 04318, Leipzig, Germany

<sup>2</sup> Dept. of Theoretical Biology, Vrije Universiteit, de Boelelaan 1085, NL-1081 HV, Amsterdam, the Netherlands

The rationale of the model and its implementation are explained in:

Martin B<sup>\*</sup>, Zimmer E, Grimm V, Jager T. Year. Dynamic Energy Budget theory meets individual-based modelling: a generic and accessible implementation. Journal Volume: pages.

\* Corresponding author, email: [btmarti25@gmail.com](mailto:btmarti25@gmail.com)

The NetLogo implementation and the user manual can be found here:

[NetLogo implementation](#).

[User manual](#).

We recommend reading the article first.

Leipzig – Amsterdam December, 2010

---

## DEB-IBM: Model Description

The model description follows the ODD protocol for describing individual-based models (Grimm et al. 2006, 2010).

### **1. Purpose**

The purpose of this model is to provide a basic framework for future work with individual-based population models that include DEB theory as a submodel for the metabolic processes of individuals.

## 2. Entities, state variables, and scales

The model includes two types of entities, individuals and the environment. Individuals are characterized by four primary state variables, henceforth referred to as DEB state variables: structure ( $L$ , unit: cm), which determines actual size, feeding rates, and maintenance costs; scaled reserves ( $U_E$ , unit: d cm), which serve as an intermediate storage of energy between feeding and mobilization processes; scaled maturity, ( $U_H$  unit: d cm), a continuous state variable which regulates transitions between the three development stages (embryo, juvenile, adult) at fixed maturity levels; and finally, mature individuals direct energy for reproduction into the 4<sup>th</sup> state variable, a scaled buffer ( $U_R$ , unit: d cm) which is converted into eggs during reproductive events. The term “scaled” in reserves, maturity, and buffer refer to the fact that in this “scaled” version of the model, the dimension of energy or mass (either as joule or moles of reserve) are scaled out (see Kooijman et al., 2008 and section 2 of the DEB-IBM User Manual).

In addition to these DEB state variables, intrinsic variation among individuals can be created by allowing a random component in some of the individuals’ 8 “standard DEB parameters”, which are shown in Table 1 and explained in more detail in the DEB-IBM User Manual. Each individual has a state variable we refer to as a “scatter multiplier” which is a log-normally distributed number, by which four of the standard DEB parameters are multiplied to get the individual-specific set of DEB parameters.

Additionally the model presented includes an optional ageing submodel based on DEB theory which includes two state variables, damage inducing compounds ( $\dot{q}$ ), and damage ( $\dot{h}$ ). Damage inducing compounds can be thought of as changed genes and affected mitochondria (affected by Reactive Oxygen Species, ROS) and damage is `wrong` proteins and other metabolic products. ROS itself has very fast dynamics so is not included. The aging process is tightly linked to energetics in that the production of damage-inducing compounds is proportional to mobilization (energy utilization). Damage inducing compounds produce damage and thereby affect survival probability. In addition to directly producing damage, damage inducing compound also can proliferate by inducing their own production (see ageing sub model for an example).

The second entity in the model is the environment, which is defined by the state variable of food density. Feeding conditions in the model can be expressed as constant feeding conditions with the state variable  $f$ , which represents the proportion of maximum assimilation which occurs by individual. Alternatively, the model has an option for simple predator-prey (or consumer-resource) dynamics, in which case the density of prey ( $X$ ) is also a state variable.

The model is non-spatial (see DEB-IBM User Manual for ways to develop spatial model versions). Time is represented continuously (ordinary differential equations), but conceptually the model is based on daily timesteps: for the numerical solution of the model equations (Euler method) users can chose the number of sub-timesteps into which one day is divided (this number is referred to as “timestep” in the program). The Euler method proved sufficiently precise, and robust, for the standard model, but if in doubt, more sophisticated solvers of ordinary differential equations can be used, either by using the R-extension of NetLogo (Thiele and Grimm, 2010), or by using the ODE solver extension of NetLogo (Thiele and Grimm, *unpublished manuscript*).

Table 1. Dimensions, state variables, and parameters of DEB-IBM. Both the formal “DEB notation” and the Netlogo notation are given for each state variable and parameter.

**Dimensions**

-	no dimension	$L$	length (of individual)	$e$	energy ( $\Xi ml^2 t^{-2}$ )
$t$	Time	$l$	length (of environment)	$T$	temperature
$\#$	Number	$m$	mass (weight)		

**State Variables and Parameters**

DEB notation	Interpretation	Dimensions	Netlogo notation
<b>State Variables</b>			
$U_E$	Scaled reserve	$tL^2$	U_E
$U_H$	Scaled maturity	$tL^2$	U_H
$U_R$	Reproduction buffer	$tL^2$	U_R
$L$	Volumetric structural length	$L$	L
$\ddot{q}$	Ageing acceleration	$t^{-2}$	q
$\dot{h}$	Hazard rate	$t^{-1}$	h
$X$	Prey density	$\#l^3$	X
<b>Standard Parameters</b>			
$\kappa$	Fraction of mobilized energy to soma	-	kap
$\kappa_R$	Fraction of reproduction energy fixed in eggs	-	kap_R
$\dot{k}_M$	Somatic maintenance rate coefficient	$t^{-1}$	k_M_rate
$\dot{k}_J$	Maturity maintenance rate coefficient	$t^{-1}$	k_J_rate
$U_H^b$	Scaled maturity at birth	$tL^2$	U_H^b
$U_H^p$	Scaled maturity at puberty	$tL^2$	U_H^p
$\dot{v}$	Energy conductance	$Lt^{-1}$	v_rate
$g$	Energy investment ratio $[E_G] / \kappa [E_M]$	-	g
<b>Ageing Parameters</b>			
$\ddot{h}_a$	Weibull ageing acceleration	$t^{-2}$	h_a
$s_G$	Gompertz stress coefficient	-	S_G
<b>Prey Dynamics Parameters</b>			
$\{\dot{J}_{XAm}\}$	Surface-area-specific max ingestion rate	$\#L^{-2}t^{-1}$	J_XAm_rate
$\{\dot{F}_m\}$	Maximum searching rate	$l^3L^{-2}t^{-1}$	f_M
-	Carrying capacity of prey	$\#l^3$	X_k
-	Growth rate of prey	$t^{-1}$	X_r
-	Volume of environment	$l^3$	volume
<b>Add My Pet Parameters (see user manual)</b>			
$[\dot{p}_M]$	Specific volume-linked somatic maint. rate	$eL^{-3}t^{-1}$	p_M
$[E_G]$	Volume-specific costs of structure	$eL^{-3}$	E_G
$z$	Zoom factor to compare body sizes	-	zoom
$E_H^b$	Maturation threshold for birth	$E$	E_H^b
$E_H^p$	Maturation threshold for puberty	$E$	E_H^p

### 3. Process overview and scheduling

Individuals update their DEB state variables based on a set of differential equations. Based on the updated DEB state variables, a set of discrete events may occur: if an organism can no longer pay maintenance costs, it dies; if an individual has matured and has enough energy to produce an offspring it will calculate the energy needed for an embryo and then produce one embryo; if the aging submodel is on, then each timestep individuals have a probability of dying which is proportional to their damage state variable,  $\dot{h}$ .

The following pseudo-code describes the scheduling of events within one timestep of the numerical solution of the model equations (see “go” procedure in NetLogo implementation):

```

For each individual
  [
    Calculate delta reserves
    If not mature [Calculate delta maturity]
    If mature?
      [
        Calculate delta reproduction buffer
      ]
    Calculate delta length
    If delta length < 0
      [
        Re-calculate structure, reserves, maturity, and buffer based on starvation rules
      ]
    If aging submodel= "on"
      [
        Calculate delta ageing acceleration
        Calculate delta hazard ]
      ]
  ]
If prey dynamics = "logistic"
  [
    Calculate delta prey density
    Update prey density
  ]
For each individual
  [
    update DEB state variables
    if mobilized energy < energy needed for maintenance
      [Die]
    If random number < prob of ageing related death
      [Die]
    If energy in Repro buffer > energy needed to reproduce
      [
        Calculate energy investment for offspring (bisection method)
        Create new offspring
      ]
  ]

```

## 4. Design concepts

### Basic principles

The model is based on the Dynamic Energy Budget theory (Kooijman 1993, 2000, 2010). An overview of the concepts can be found in Kooijman (2001) or Nisbet et al. (2000). The theory is based on the general principle that metabolic processes are proportional to surface area or body volume and a full balance for mass and energy.

### Emergence

Traits of the individual and structure and dynamics of the population emerge from the properties of metabolic organization and indirect interactions of individuals via competition for food.

### Adaptation

The model does not include adaptive behavior; in particular, DEB parameters vary among individuals but remain constant over an individual's lifespan. Consequently, the design concepts "objectives", "learning", "prediction", and "sensing" do not apply to this model.

### Interaction

When food dynamics submodel is set to logistic, individuals interact indirectly via competition for food.

### Stochasticity

In the standard DEB model the only inherent source of stochasticity comes from the ageing submodel. Additionally stochasticity can be included by allowing individuals to vary in some of their DEB parameters. This method is justified because experiments often find that repeated physiological measurements of individuals are less variable than those between individuals. We followed the method outlined in Kooijman (1989) where the surface-area-specific maximum assimilation rate of individual ( $i$ ) is given by multiplying the species specific  $\{J_{EAm}\}$  with the individual-specific scatter multiplier  $SM_i$ . The "scatter multiplier" is a log-normally distributed random number with a standard-deviation which is user defined. However, since DEB-IBM is based on the scaled, not the standard, DEB model where  $\{J_{EAm}\}$  is scaled out of the model,  $\{J_{EAm}\}$  is a "hidden" parameter affecting four other scaled and compound parameters. We describe these inter-relationships in detail in section 2 of the DEB-IBM User Manual.

### Observation

In the default model we include several output plots and histograms to monitor the population dynamic of the modeled species. These include a plot of population density, a plot of prey density, and a plot of the stage class density (embryo, juvenile, and adult). Additionally there are three histograms: length distribution, and scaled reserve density ( $e$ ) for both juveniles and adults. Ultimately the user can record and plot any individual- or population-level variable of interest. (Note that in NetLogo the data presented in plots can easily be exported to text files; see NetLogo User Manual).

## 5. Initialization

The DEB parameters in the default model come from the so-called "add\_my\_pet" database for the species *Daphnia magna*. The foraging submodel (explained below in the section "Submodels") was set to logistic with parameters of:  $\{J_{XAm}\} = 1$ ,  $F_m = 1$ ,  $X_r = 0.5$ ,  $X_k = 2$ , and

volume = 1. This simulates a scenario where the carrying capacity of the prey population is twice the half saturation-constant, which is given by  $\{J_{XAm}\} / F_m$ . In the default version of DEB-IBM, we are not modeling any specific unit of prey. Prey could be in cells per ml, grams of carbon per liter, ect.. Thus the value we select for the absolute value of  $\{F_m\}$  does not affect prey dynamics, but rather its relation to  $X_k$  and  $\{J_{XAm}\}$ . In general the smaller  $\{J_{XAm}\}$  is in relation to  $X_k$ , the higher the population density, as  $\{J_{XAm}\}$  determines how quickly the prey is depleted, and  $X_k$  determines the maximum capacity of prey per unit of “volume”. Because the half saturation coefficient,  $K$ , is given by  $\{J_{XAm}\} / \{F_m\}$  the ratio between these two parameters effects how sensitive individual assimilation rate is over the range of prey densities. Unless compensating mechanisms are considered (inducible defenses, spatial heterogeneity, multiple prey types) a low  $K$ , in relation to  $X_k$  generally results in unstable predator prey dynamics. This is general to population models (classical, matrix, and IBM) and is known as the “paradox of enrichment”.

Simulations are initiated with the creation of 10 embryos with  $L = 1.0 \times 10^{-5}$ ,  $U_E = 0.004$ ,  $U_H = 0$ ,  $U_R = 0$ ,  $\ddot{q} = 0$ , and  $\dot{h} = 0$ . The initial value of  $L$  should represent the initial structural length of an individual, which is very small for newly created embryos (newly created embryos consist nearly only of reserves). The initial embryos are created with enough energy to reach the juvenile stage with a scaled reserve density equal to 1 (maximum reserve density). The amount of initial reserves required to meet this condition are dependent on the DEB parameters of the species and are determined in the setup procedure via the bisection method (see DEB-IBM User Manual for details).

## 6. Input data

The model does not include input data representing external driving processes.

## 7. Submodels<sup>1</sup>

### Calculate delta energy reserves

The change in energy reserves  $U_E$  of an individual in a time step is determined by the difference in scaled assimilation  $S_A$  and mobilization  $S_C$  fluxes.

$$\frac{d}{dt}U_E = (S_A - S_C)$$

where

$$S_A = fL^2$$

---

<sup>1</sup> Note: The formulas used in our implementation have been algebraically rearranged, reduced (using compound parameters), and scaled with the aim of reducing the amount and types of data needed to parameterize the model for a species. However as a result of this modification, some of the resulting formulas and parameters used in DEB-IBM may not seem intuitive. To facilitate a better understanding we provide an in-depth guide for the derivation of our “reduced” formulas used in DEB-IBM from the standard DEB theory in section 2 of the User Manual. Below we provide all formulas as implemented in DEB-IBM and a brief rational.

and

$$S_C = L^2 \frac{ge}{g+e} \left( 1 + \frac{L\dot{k}_M}{\dot{v}} \right)$$

where

$$e = \dot{v} \frac{U_E}{L^3}$$

Under constant food conditions the scaled functional response,  $f$  is user-defined. For example, an  $f$  of 1 represents *ad libitum* feeding, and an  $f$  of 0.8 represents the scenario where feeding occurs at 80% of the maximum rate. If  $f$  is set to 0 no feeding occurs. If the logistic food-dynamics are turned on,  $f$  is a function of food density.

$$f = \frac{X}{K+X} \text{ for } U_H > U_H^b$$

where

$$K = \{J_{XAm}\} / \{F_m\}$$

Because embryos do not feed exogenously

$$\text{when } U_H < U_H^b \quad f = 0$$

or when scaled maturity is less than the maturity needed for hatching,  $U_H^b$ , feeding will not occur and thus the assimilation flux will be zero and the change in reserves is reduced to:

$$\frac{d}{dt} U_E = -S_C$$

*Rationale:*

Unlike most bioenergetics models used in fisheries (Chipps and Wahl 2008), DEB theory includes a state variable “reserves” which acts as an intermediate between the feeding and mobilization process. The inclusion of a reserves state variable apart from structure in DEB theory was driven by several observations (Kooijman 2010). Reserves allow for metabolic memory, i.e. the metabolic behavior of individuals is not dependent on the current food availability, but rather the “recent” feeding history of an individual. For example animals can continue to grow for a short period of time when food has been removed from their environment. Additionally, reserves help explaining observed body size scaling relationships (Kooijman 2010).

### Calculate delta maturity

Individuals begin with a maturity level  $U_H$  of 0, which increases each timestep:

$$\text{when } \frac{d}{dt} U_H = ((1 - \kappa) S_C - \dot{k}_J U_H) \quad U_H < U_H^p$$

else

$$\frac{d}{dt}U_H = 0$$

Transitions between development stages occur at set values of maturity. An embryo which feeds exclusively on reserves becomes an exogenously feeding juvenile when  $U_H > U_H^b$  and a reproducing adult when  $U_H > U_H^p$ . Once puberty is reached, maturity is fixed and energy previously directed towards maturity is now allocated to the reproduction buffer.

*Rationale:*

Non-mature individuals divert mobilized energy from reserves between competing functions of growth and development, with the proportion  $1-\kappa$  of mobilized reserves allocated to development. Individuals first pay maintenance costs associated with maintaining their current level of maturity (the maturity maintenance rate coefficient,  $\dot{k}_J$ , multiplied by the current level of maturity,  $U_H$ ) from the mobilized reserves directed toward development from the mobilized reserves  $[(1-\kappa)S_C]$ . The remainder represents the increase in development during a timestep.

### Calculate delta repro buffer

When an individual has reached puberty, energy from the maturity flux is diverted into a reproduction buffer,  $U_R$ .

$$\frac{d}{dt}U_R = ((1-\kappa)S_C - \dot{k}_J U_H^p) \text{ for } U_H > U_H^p$$

else

$$\frac{d}{dt}U_R = 0$$

*Rationale:*

This submodel is basically the same as for the delta maturity calculation, but is calculated only for mature individuals. Because scaled maturity no longer increases after puberty has been reached, the maturity maintenance rate coefficient,  $\dot{k}_J$ , is multiplied by maturity at puberty parameter,  $U_H^p$ . Thus the energy that accumulates in the reproduction buffer in a given time step is the difference between mobilized energy allocated towards reproduction and the maturity maintenance costs.

### Calculate delta length

During a timestep energy needed for somatic maintenance costs are paid from mobilized energy allocated for soma. The remainder is converted from reserve to structural length. Under non-starvation conditions:

$$\frac{d}{dt}L = \frac{1}{3} \left( \frac{\dot{v}}{gL^2} S_C - \dot{k}_M L \right)$$



The parameter  $\kappa$ , which determines the fraction of mobilized energy directed to the soma is not directly in this formula, however,  $\kappa$ , is in the compound parameter  $g$  (see section 2.4 of the user manual). If mobilized energy allocated towards somatic growth and maintenance is insufficient to pay somatic maintenance costs, a deviation from the standard rules is necessary. In DEB theory, this situation occurs when scaled reserve density is insufficient to maintain the length of an individual and coincides with the point when the reserve density,  $e$ , falls below scaled length ( $l$ ), which is the length of an individual divided by the maximum length an individual can growth to ( $L_M$ ).

$$e < \frac{L}{L_M}$$

The maximum length of an individual is a function of 3 of parameters (energy conductance,  $\dot{v}$ , somatic maintenance rate coefficient,  $\dot{k}_M$ , and energy investment ratio,  $g$ ).

$$L_M = \frac{\dot{v}}{\dot{k}_M g}$$

When reserve density ( $e$ ), falls below scaled length ( $l$ ) for an individual, they will respond by setting growth to zero and diverting enough energy headed to either maturity (for juveniles) or reproduction buffer (for adults) to pay somatic maintenance. Because the organisms do not grow in the scenario, mobilization of reserves is simplified to:

$$S_C = eL^2 \text{ when } \frac{d}{dt}L = 0$$

We first need to calculate how much energy must be diverted from maturity or reproduction mobilization flux to pay maintenance costs. Setting growth to zero in the above differential equation describing growth in length yields:

$$\kappa S_C = \frac{\dot{k}_M \kappa g}{\dot{v}} L^3$$

This is the amount of energy needed to pay somatic maintenance. The remaining energy is diverted to the maturity or reproduction buffer:

$$\frac{d}{dt}U_H = (1-\kappa)S_C - \dot{k}_J U_H^P - \kappa L^2 \left( \frac{L}{L_M} - e \right) \text{ when } U_H < U_H^P$$

$$\frac{d}{dt}U_R = (1-\kappa)S_C - \dot{k}_J U_H^P - \kappa L^2 \left( \frac{L}{L_M} - e \right) \text{ when } U_H > U_H^P$$

Notice the  $U_H$  in the maturity maintenance part of the formula  $\dot{k}_J U_H$ , is replaced by  $U_H^P$  in the second formula for adults ( $U_H > U_H^P$ ). This is because  $U_H^P$ , is the maximum value of  $U_H$  and represents the point where no further energy is invested to maturity. In other words when  $U_H = U_H^P$  an individual is completely developed or mature.

These starvation dynamics continues until either the condition:  $e < \frac{L}{L_M}$  is no longer true, and an individual resumes normal mobilization dynamics, or until  $\frac{d}{dt}U_H$  or  $\frac{d}{dt}U_R$  become negative. More simply, when an individual cannot mobilize enough energy to pay maintenance costs even using all available energy which would normally be diverted towards maturity or reproduction it dies.

*Rationale:*

When mobilized reserves allocated to the soma are insufficient to pay somatic maintenance costs, animals may respond in many ways, which can be represented in DEB (see Kooijman 2010 for discussion of starvation strategies). Here, we present one fairly general way which does not require any new parameters. For modeling a specific species, consideration should be given to which starvation strategy is most appropriate.

### Reproduction submodel

In the standard DEB model mature individuals invest exactly the amount of energy into an egg that is needed for the offspring to have the same scaled reserve density ( $e$ ) at the time of hatching as the mother at conception; in this way, maternal effects are taken into account. In our implementation of the DEB model, individuals reproduce when they have enough energy to produce one offspring which meets this condition. To determine when an individual can reproduce, each mature individual creates a hypothetical egg with the initial energy reserves set to the available energy in the reproduction buffer  $U_R\kappa_r$  (where  $\kappa_r$  is the conversion efficiency from buffer to embryo) of the mother. The embryonic period of the hypothetical offspring is then simulated until one of two conditions is met. If the scaled reserve density ( $e$ ) of the hypothetical offspring falls below that of the mothers, then the simulation is stopped and the mother will not reproduce in that timestep. If the hypothetical embryo reaches the energy needed for birth, then the mother will produce an egg in the current timestep.

The next phase of the reproduction submodel is to determine the exact amount of energy a mother will invest in the egg (the remainder stays in the reproduction buffer). This is determined numerically using the bisection method. The initial bounds for the bisection method are set to 0 and  $U_R\kappa_r$  of the mother. Simulations are run until the offspring is within 5% of the mother's scaled reserves in the simulated timestep when maturity hits the threshold for birth ( $U_H > U_H^b$ ; see User Manual for details). An egg is then created with initial reserves set to the estimation from the previous step. The egg will hatch and thus begin exogenous feeding when  $U_H > U_H^b$ .

### Optional submodels

#### Prey dynamics submodel

If the "logistic" option is selected for prey dynamics type, prey follow a simple logistic growth minus the loss due to predation.

$$\frac{d}{dt}X = (r_X X (1 - (X / K_X)V - P_X) \dot{k}_T$$

where

$$P_X = \sum_i fL_i^2 \{J_{XAm}\}_i$$

### Ageing submodel

Users can select whether the DEB aging submodel is turned on or off. The basic premise of the DEB aging submodel is that damage inducing compounds are created at a rate proportional to reserve mobilization. Damage inducing compounds induce more damage inducing compounds also at a rate proportional to mobilization. The hazard rate for mortality due to ageing of an individual is proportional to density of the accumulated damage in the body. Additionally the concentration of both damage inducing compounds and damage are assumed to be diluted via growth ( $\dot{r}$ ). The ageing submodel includes two new parameters the Weibull ageing acceleration parameter,  $\ddot{h}_a$  and Gompertz stress coefficient,  $s_G$ . To reduce the total number of parameters, the equations for damage-inducing compounds, damage and hazard rate are scaled and combined to two ODE's, for "scaled acceleration" ( $\ddot{q}$ ) and hazard rate ( $\dot{h}$ ):

$$\frac{d}{dt} \ddot{q} = \left( \ddot{q} \frac{L^3}{L_m^3} s_G + \ddot{h}_a \right) e^{\left( \frac{\dot{v}}{L} - \dot{r} \right) - \dot{r} \ddot{q}} \quad \text{where } \dot{r} = \frac{3}{L} \frac{d}{dt} L$$

$$\frac{d}{dt} \dot{h} = \ddot{q} - \dot{r} \dot{h}$$

When the aging submodel is turned off individuals have a set probability of dying each day determined by the parameter "background-mortality".

#### *Rationale:*

In our model ageing processes are linked tightly to energetics as the production of damage inducing compounds are proportional to mobilization. The premise of this assumption is that the production of free radicals or other reactive oxygen species is proportional to the use of dioxygen in metabolic process. The inclusion of energetics in the ageing process allows differences in ageing of animals in feeding conditions or physiological phenotypes to be explained without altering ageing parameters. For example, longer lifespans of mice reared at lower food densities are accounted for by the DEB ageing model as mice fed high food had higher mobilization which led to a high concentration of damage inducing compounds, damage, and ultimately shorter lifespans (Kooijman 2010). Additionally the differences in survival between male and female daphnia are accounted for by their different DEB parameters (Kooijman 2010).

## Literature Cited

Chipps, S. R. and D. H. Wahl. (2008) Bioenergetics Modeling in the 21st Century: Reviewing New Insights and Revisiting Old Constraints. *Transactions of the American Fisheries Society*, **137**, 298-313.

- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S., Huse, G., Huth, A., Jepsen, J. U., Jørgensen, C., Mooij, W. M., Müller, B., Pe'er, G., Piou, C., Railsback, S. F., Robbins, A. M., Robbins, M. M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R. A., Vabø, R., Visser, U., and D. L. DeAngelis. (2006) A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, **198**, 115-126.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, G., Giske, J., and S. F. Railsback. (2010) The ODD protocol: a review and first update. *Ecological Modelling*, **221**, 2760-2768.
- Kooijman, S. A. L. M., N. v. d. Hoeven and D. C. v. d. Werf. (1989) Population consequences of a physiological model for individuals. *Funcional Ecology*, **3**, 325-336, 1989.
- Kooijman, S. A. L. M. (1993) *Dynamic energy budgets in biological systems. Theory and applications in ecotoxicology*. Cambridge University Press.
- Kooijman, S. A. L. M. (2000) *Dynamic Energy and Mass Budgets in biological systems*. Cambridge University Press.
- Kooijman, S. A. L. M. (2001) Quantitative aspects of metabolic organization; a discussion of concepts. *Philisophical Transactions of the Royal Society B.*, **356**, 331-349.
- Kooijman, S. A. L. M., T. Sousa, L. Pecquerie, J. Van der Meer and T. Jager. (2008) From food-dependent statistics to metabolic parameters, a practical guide to the use of Dynamic Energy Budget theory. *Biological Reviews*, **83**, 533-552.
- Kooijman, S. A. L. M. (2010) *Dynamic Energy Budget theory for metabolic organisation*. Cambridge University Press.
- Nisbet, R. M., E. B. Muller, K. Lika, and S. A. L. M. Kooijman. (2000) From molecules to ecosystems through Dynamic Energy Budget models. *Journal of Animal Ecology*, **69**, 913-926.