Appendix H: ODD of the DEB-IBM model

The ODD is available in the "Info" section of the NetLogo code, found at
http://modelingcommons.org/browse/one_model/6201.

MODEL PRESENTATION

The present DEB-IBM (Dynamic Energy Budget - Individual-Based Model) was built to simulate and predict population dynamics in an endemic common benthic species of the Kerguelen Plateau (sub-Antarctic region), the sea urchin *Abatus cordatus*. It upscales the individual mechanistic DEB model to the population level, enabling to model the population dynamics through time as a product of individual physiological responses, and to predict the species response to a changing environment through comparisons between sites and between predicted future scenarios. The main objective of this work was to develop the model using the available data for this species living in a remote environment that is impacted by climate change and where logistical challenges strongly hinder the scientific research.

How to run this model ?

A few simple steps are necessary to run this model under its basic implementation:

1/ Download the model and the environmental files from the ''Files'' tab in the NetLogo modeling commons
(http://modelingcommons.org/browse/one_model/6201#model_tabs_browse_files).
For the basic implementation, the two files needed are *"temp_time_monthavg_Halage.txt"* for temperatures and *"inputRSces_M_f_Delille.txt"* for resources. Make sure the model (.nlogo) and the data (.txt) files are stored in the same folder on your computer.

2/ Once you have opened the model (.nlogo), the interface is generally the first thing that is visible. Navigation between the interface, the information page, and the code of the model is done through the three tabs at the top of the software ('Interface', 'Info', 'Code').
Make sure that the following elements are selected in the interface:

- *Sites*: 'Anse du Halage'
- *projection*: 'present'
- *future*: 'mixed temp & food'
- *sensitivity*: 'resistant'
- *competition*: 'On'
- *run_time*: '210'
- *cv*: '0.1'
- *add-my-pet?*: 'Off'

Also ensure that none of the green boxes ('input paramaters') is empty. If any of them is empty, switch the *add-my-pet?* button 'On' and fill the relevant boxes with the basic DEB parameters for *A. cordatus* as taken from the Add-my-Pet database
(https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Abatus_cordatus/
Abatus_cordatus_res.html): $[\dot{p}_M]$, E_H^b, E_H^p, $[E_G]$ and L_m, which correspond to these boxes respectively: p_M, E_H^b, E_H^p, E_G, zoom.

Except in the aforementioned case, do not modify any of the parameters in the green boxes placed under the line « Input parameters » on the interface.

3/ Click on the purple *setup* button. This initializes the model, and should barely take a second on an average computer. A sure way of knowing the model has finished setup, is that color shapes appear in the small black square that is on the bottom-right of the purple buttons.

4/ Once setup is finished, click on the purple *go* button. This will run the model for the simulated duration input in the *run_time* box (number of years). Clicking on the *go* button again before the end of the simulation will pause the model, clicking on it after the end of the simulation will continue the simulation without a temporal limit. The *go once* button will only run the model for a single loop, that is a simulation of one month.

5/ The model can be run for future projections with different combinations of food and/or temperature scenarios. For this, select in the interface the desired RCP scenario under *projection* and the wanted combination under *future*. Three types of sensitivity to high temperature are also available under *sensitivity* (see « Check temperature » submodel in the ODD below for a short explanation of the difference between the three types).

For now, the model only fully works if the site Anse du Halage is selected. Sites Port Couvreux and Ile Haute can also be selected, however the site-specific data is only available for temperature and not for resources. Thus, if one of those two sites is selected, the file for the resources data will be that of Anse du Halage. This is merely to test the model for different temperature data using real time-series records rather than future projections.

NB: Here again, make sure that the relevant temperature files (*"temp_time_monthavg_Couvreux.txt"* or "*temp_time_monthavg_Haute.txt* »), also available in the ''Files'' tab in the NetLogo modeling commons) are stored in the same folder as the model.

Other things to keep in mind in this implementation:-

- The temporal resolution is a monthly interval.
- Temperature and functional response f are in the form of time-series. (To test with constant and DEB standard values, uncomment the corresponding lines at the beginning of the *go* procedure in the code).
- This species lives in waters of 5°C in average, however the upper limit of the Arrhenius relationship is not available to model *Abatus cordatus* physiological response to higher temperatures. Because of this, the mortality due to temperature was manually forced in the model using survival data obtained during an experiment led in Kerguelen in November 2018.

MODEL DESCRIPTION

Here is a schematic representation of the DEB-IBM model and a short summary description (the letters in brackets refer to the figure):
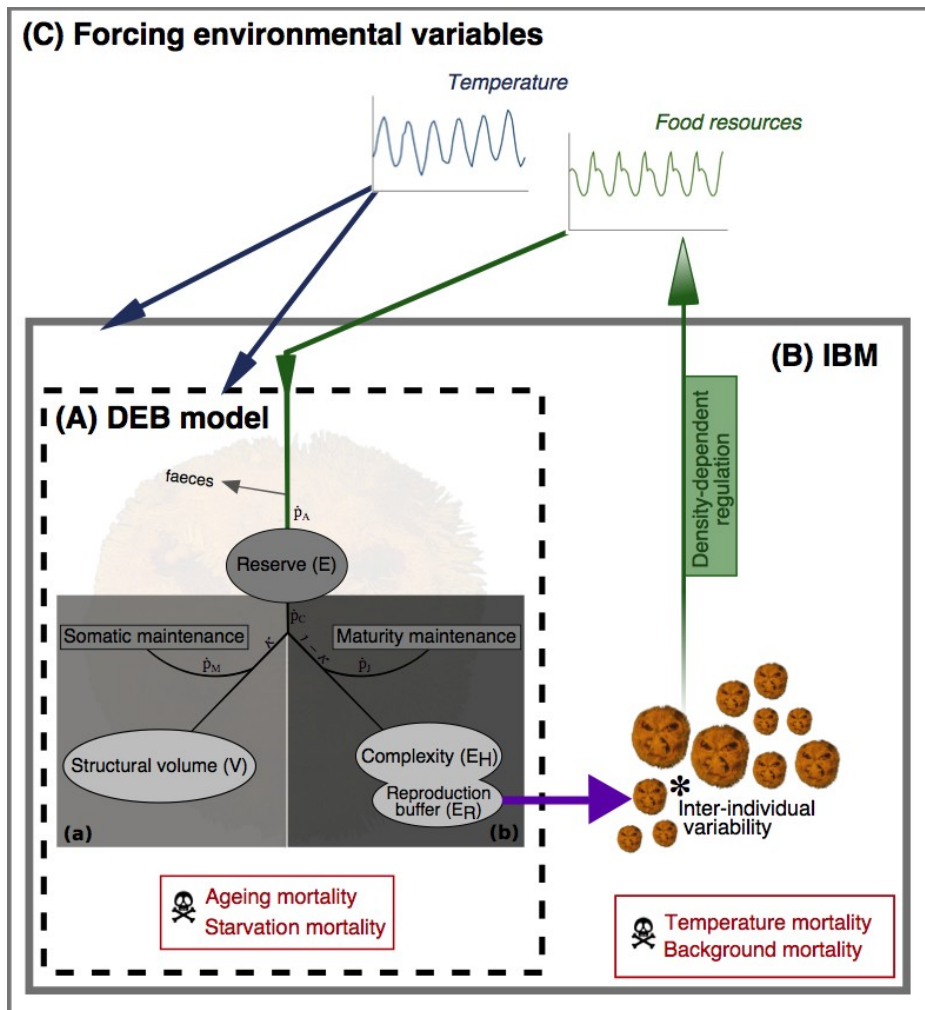
Individuals (A) undergo development through the DEB model and reproduce (purple arrow). Altogether and with a slight inter-individual variability in DEB parameters (*), they form the population of the IBM (B) which undergoes population-specific processes (temperature and background mortalities) at the scale of a simple square metre patch at the reference site (C). The IBM population is embedded within this specific environment, whose environmental conditions (temperature and food resources) affect individual and population dynamics. Additionally, the population influences the resources availability following a density-dependence regulation.

Below is the description of the model following the ODD (Overview, Design concepts and Details) protocol from Grimm et al. (2010), where information on the following characteristics can be found:

| 1. Purpose | Short presentation of the objective of the model |

2. **Entities, state variables & scales** Parameters with their DEB notation, code notation, dimension and
signification

                 Types of entities in the model, their state variables
                 Temporal resolution and temporal extent of the model, spatial resolution

3. **Process overview & scheduling** Pseudo-code of a simulation (what the model does in one 'go once'
simulation)

                 Order in which agents execute commands, when variables get updated
                 How time is represented in the model, presentation of calendars and timers

4. **Design concepts**
- Basic principles   Underlying DEB theory and principles
- Emergence   Emergent and imposed results
- Adaptation   Adaptative traits of individuals
- Interaction   Individuals interactive behaviours
- Stochasticity   Randomization in processes
- Collectives   How individuals are grouped under types of entities, specific characteristics
- Observations   Outputs of the model for results or tests

5. **Initialisation**   Elements to select and parameters to input for initialisation
                 Initial state of the model at setup
                 Origin of initial parameters, Initialisation of individuals
                 What differs from one initialisation to another

6. **Input data**   Data taken from external files, How the files are compiled and read
                 Specific data for the standard basic model (Anse du Halage)

7. **Submodels**   Detailed description of each submodel, with equations and processes:
- Update calendar
- Update environmental variables
- Competition and f
- Convert parameters with TC (temperature correction factor)
- Change in reserve
- Change in maturity or reproduction buffer
- Change in structural length
- Starvation
- Ageing
- Update individuals
- Update reproduction and birth timers
- Reproduction
- Calculate GSI
- Background mortality
- Check temperature

1. Purpose

- Population monitoring
- Update time

The model was developed from the individual mechanistic Dynamic Energy Budget (DEB) model to
study the response of the populations of the sea urchin *Abatus cordatus*, endemic to the Kerguelen

2. Entities, state variables and scales

Plateau (sub-Antarctic region), to changes in environmental conditions (temperature and resources), through comparisons between sites and between predicted future scenarios.

DEB notation	Notation in the code	Dimension and description
e	e_scaled	(-) scaled reserve density per unit of structure, e = [E]/[E$_m$]
E_H^b	E_H^b	(e) maturity at birth
E_H^p	E_H^p	(e) maturity at puberty
[E$_G$]	E_G	(e·L^{-3}) volume-specific costs of structure
g	g	(-) energy investment ratio
h	h_rate	(t^{-1}) specific death probability rate
∂h	dh_rate	(-) change of hazard rate in time
$\dot{h}_a$	h_a	(t^{-2}) Weibull ageing acceleration
$\varkappa$	kap	(-) fraction of mobilised reserve allocated to soma
$\varkappa_R$	kap_R	(-) reproduction efficiency
$\dot{k}_M$	k_M_rate	(t^{-1}) somatic maintenance rate coefficient
$\dot{k}_J$	k_J_rate	(t^{-1}) maturity maintenance rate coefficient
L	L	(L) structural length
∂L	dL	(-) change of structural length in time
L$_w$	Lphy	(L), physical length (L/∂_M), with ∂_M being the shape coefficient (-)
L$_b$	L_b	(L) structural length at birth
L$_m$	zoom	(L) maximum volumetric length
[$\dot{p}_M$]	p_M	(e·L^{-3}·t^{-1}) specific volume-linked somatic maintenance rate
$\ddot{q}$	q_acceleration	(t^{-2}) ageing acceleration
$\partial \dot{q}$	dq_acceleration	(-) change of ageing acceleration in time
S$_A$	S_A	(L^2) assimilation flux (scaled)
S$_C$	S_C	(L^2) mobilisation flux (scaled)
s$_G$	sG	(-) Gompertz stress coefficient
s$_M$	s_M	(-) acceleration factor
U$_E$	U_E	(t·L^2) scaled reserves, U$_E$ = E / {$\dot{p}_{Am}$}
∂U_E	dU_E	(-) change of scaled reserves in time
U_H^b	U_H^b	(t·L^2) scaled maturity at birth
U_H^p	U_H^p	(t·L^2) scaled maturity at puberty
U$_H$	U_H	(t·L^2) scaled maturity
∂U_H	dU_H	(-) change of scaled maturity in time
U$_R$	U_R	(t·L^2) scaled energy in reproduction buffer
∂U_R	dU_R	(-) change of energy in reproduction buffer
$\dot{v}$	v_rate	(L·t^{-1}) energy conductance
y$_{VE}$	y_VE	(mol/mol) yield of structure on reserve
Other variables	**Notation in the code**	**Dimension and description**
f	f	(-) scaled functional response
K	car-cap	(#) carrying capacity
density	pop_density	(#/m^{-2}) current population density
competition	food_compet	quantification of the scale of competition
TC	TC	(-) temperature correction factor
GSI	GSI	(-) gonado-somatic index
eggs	eggs	(#) number of eggs per female
Ri	Ri	(#) reproductive output (number of juveniles born per female)
Scatter multiplier	scatter-multiplier	(-) parameter used to put a random variation in individual parameters

The model includes two types of entities: individuals and the environment. Individuals are divided into 4 types of sub-agents, depending on life-stage and sex: embryos, juveniles, adult males and adult females. Life-stages are considered using DEB definitions. Individuals are characterized by four primary state variables, based on DEB theory (Kooijman 2010): scaled reserve (U$_E$), structural length (L), scaled maturity (U$_H$) and scaled reproduction buffer (U$_R$). Additional state variables for individuals are age (in months and in years), ageing acceleration ($\ddot{q}$) and

death probability rate (ḣ). State variables in DEB are originally dependent on energy (unit of Joules), but in order to simplify the calculations of differential equations so that they do not require measurements of energy, each state variable was discarded of their energy unit by dividing with the maximum surface-area specific assimilation rate $\{\dot{p}_{Am}\}$ (dimension $eL^{-2}t^{-1}$) following Martin et al. (2010) and Kooijman (2010). Females have supplementary attributes linked to reproduction processes for which the state variable is the gonado-somatic index (GSI), that is the ratio of gonad weight over the weigth of the entire body. Finally, each individual has a variable called scatter-multiplier, used to implement a slight variation in three standard DEB parameters (U_H^b, U_H^p, g) and initial energy reserve at birth (U_E_0yo). This scatter-multiplier is the exponential of a number taken randomly on a normal distribution of mean 0 and standard deviation cv (set by the user in interface).

The environment in the model is characterized by two state variables, monthly average temperature (T, unit: °C) and monthly resources availability represented by the proportion of food an individual can intake on a scale of 0 to 1 (f, no dimension). Values for these variables are input into the model from external files, as time-series of monthly values. Temperature data was collected from existing thermo-recorders on the corresponding sites (implemented by the PROTEKER programme, http://www.proteker.net/?lang=en), while resources data comes from the publication by Delille & Bouvy (1989) for the site Anse du Halage.

Models provide results at a monthly resolution, over a temporal extent that can be modified by the user in the interface (example set at 210 years). The first ten years are assumed to be the model initialisation phase and should be removed for the analysis of results. Changes are applied to individuals on a monthly basis and thus each update corresponds to the state of the system at the end of the displayed month. In this implementation, the model runs on one single patch of environment representing one square meter, and thus density of population is equal to number of individuals present in the model. Movements of individuals are not taken into account, and each individual born on the patch grows and dies on that same patch. There is no information about water movements in the area, and the species is known to mostly feed on sediment matter. This model is non-spatial, and connectivity between the patches (e.g. for food or individual movements) is assumed to have little enough significance to be absent from this model.

At each timestep, the model runs the following commands in that order:

3. Process overview and scheduling

```
Reset the death counts
 Update calendar

 (For each patch:

        Update environmental variables
        If competition ON [
                Calculate competition
        ]
        Calculate f
 )

 (For each individual:

        Remove if marked as deceased
        Convert relevant parameters with temperature correction factor
        Calculate change in reserve
        If not mature [
                Calculate change in maturity
        ]
        If mature [
                Calculate change in reproduction buffer
        ]
```

4. Design concepts

ong
for
han
s a
ons
th,
nd
as
population death rates and density-dependent processes. The emerging state of the population is then observed, and compared between different scenarios of environmental variations.

EMERGENCE

The model illustrates the evolution of the population structure following the response of the individuals to the environmental conditions input. Metabolic responses, life-stages, ability to reproduce, starvation and ageing processes of the individuals, emerging from the mechanistic representation of their development, affect the population structure and average characteristics. A background mortality rate and a mortality caused by above normal temperatures are forced into the model, and the same reproductive output is imposed to all females that are able to reproduce.

ADAPTATION

Agents do not have an adaptive behavior. Individual traits vary among individuals in a population, but each individual carry the same traits along their entire lifespan and do not change nor learn from the

events they experience or from each other. Consequently, the design concepts "objectives", "learning", "prediction", and "sensing" do not apply.

INTERACTION

Individuals do not have any direct interaction. They only affect each other indirectly, as the size of the population influences the resources availability and thus the capacity of each individual to access food.

STOCHASTICITY

In the model, stochasticity is used in the ageing submodel: there is a 50% chance that the ageing process is activated and observed for the individual. This stochastic element can be modified in the code by changing the numbers x and y in the 'update individual' procedure. Stochasticity is also implemented in four of the initial variables for each individual (scaled maturity at birth, scaled maturity at puberty, energy investment ratio, energy reserve at birth), using the scatter-multiplier, the exponential of a number taken randomly on a normal distribution of mean 0 and standard deviation cv (set by the user in the interface of the model, at 0.1 for the standard model). (taken from Martin et al. 2010, Kooijman 2010).

COLLECTIVES

The individuals are grouped under a particular type of entity depending on their life-stage and sex, and update their life stage along time: beginning at the "juveniles" type (from around 0 to 2 years old), they are then belonging to the "males" or "females" type after reaching puberty (around 3 years old). The age at which a juvenile reaches puberty is an emergent property of its development. The sex is arbitrarily and randomly imposed on the individual that becomes an adult so that the sex-ratio (males/females) of the population is around 0.99. Depending on which group they belong to, some variables are different: juveniles do not modify their reproduction buffers, males and female do not modify their maturity compartment, females possess some proper variables such as GSI (Gonado-somatic index), eggs (number of eggs produced) and Ri (reproductive output). These collectives do not emerge from individual behaviour, but instead are implemented by the modeller in order to distinguish the life stages and sex of the individuals.

OBSERVATIONS

The main output of the model are plots of the population structure with densities of population at the different life-stages, plots of the cumulative counts of individual deaths (and proportions of associated causes), plots of mean values in state variables U_R, U_E and L and change in those state variables (∂U_R, ∂U_E and ∂L) for the different individual types. These plots allow to observe the response of the population to contrasting environmental conditions and individual metabolic responses in the population in relation to these environmental conditions. Additionally, plots of the mean age at death

5. Initialisation

of individuals dying due to the ageing submodel were used to calibrate the ageing submodel itself.

For the standard model, the following elements must be selected in the interface:

- *Sites*: 'Anse du Halage'
- *projection*: 'present'
- *future*: 'mixed temp & food'
- *sensitivity*: 'resistant'
- *competition*: 'On'
- *run_time*: '210'

- *cv*: '0.1'

The initial DEB parameters can be calculated by the model if the *'add-my-pet?'* switch is set to ON in the interface and the basic DEB parameters $[\dot{p}_M]$, E_H^b, E_H^p, $[E_G]$ and L_m for the species as taken from the Add-my-Pet database are input into the relevant boxes (respectively: p_M, E_H^b, E_H^p, E_G, zoom).

The standard model is run for 210 years in total for the site Anse du Halage under present-day conditions, with a population sensitivity set to 'resistant' and competition affecting resources availability. At setup, the values for the temperature and f at the site are taken from the time-series data found in the input files and compiled into lists usable by the model. The model is initialized with environmental conditions of October (month_time 10). If the model is set for future projections, the values are modified according to the chosen scenario (i.e. either one of RCP 2.6 and RCP 8.5 with food only, temperature only or food and temperature combined).

The carrying capacity is set at 200 ind./m² and the proportion of females at 0.5.

Initial parameters are based on *A. cordatus* DEB model parameters, developed in Guillaumot (2019). Two simulation procedures are run for the initialisation of individuals: (1) a simulation of embryonic development to determine the initial reserve at birth, and (2) a simulation of the development of one individual from 0 till 5 years old at constant f and temperature values.

The first simulation uses a bisection method to determine the initial reserve at birth. The loop simulates the embryonic development from conception till birth, while testing for different scaled reserve *e* at conception. When the scaled reserve reaches the aimed value after a few loops of development, there are two possible situations: either the development is before or past the birth stage, and thus the loop is reset with new values of initial scaled reserve *e* set accordingly and the simulation relaunched, or the development is at birth stage and the value of scaled reserve *e* that was obtained is saved.

The second simulation starts off where the first one finishes, using the resulting reserve density at birth. It runs a loop for the development of the individual from birth till five years old, with standard parameters and a constant functional response f = 1. The simulation keeps track of the age of the individual, and for each year the values for the state variables are set aside and the simulation continues until the following year. These values are stored in variables and will be used to initialize models.

When running a model, an initial population of 120 individuals is created and contains a similar proportion of the individuals belonging to six age classes from 0 to 5 years old. Each of these individuals receive the set of parameters corresponding to its age class (variables stored in the 'second simulation' mentioned in the above paragraph), with stochasticity applied on some of these parameters (see section 'Stochasticity').

6. Input data

Each individual sets its calendars with GSI_time at 5 and repro_time at 7, and females are given initial values of 0.03 for their GSI and set their birth_time timer at 0.

The model reads environmental variables from input .txt files containing monthly time-series of food resources (from Delille & Bouvy 1989) and temperatures (PROTEKER programme IPEV n°1044). The text files contain an ordered list of values (see below for Anse du Halage data). The temperature file contains 72 values of monthly average temperatures corresponding to temperature records from October 2012 to September 2018. The food resources file contains 12 values, taken from the measurements of organic carbon content in sediments published in Delille & Bouvy (1989) and scaled by the maximal value to create a proxy of f, contained between 0 and 1.

Data for resources and temperatures (excerpt) at Anse du Halage:

```
Resources:
month   f value
01      0.748
02      0.775
03      0.756
04      0.712
05      0.559
06      0.477
07      0.432
08      0.432
09      0.477
10      0.648
```

```
   Temperatures:
time    mean temperature
0       3.576178523
1       4.272769444
2       5.693903226
3       6.680989247
4       7.540075893
5       7.95569852
6       7.359872222
7       5.870103495
8       4.220568056
9       3.152399194
10      2.534522849
11      2.528454167
12      2.880237584
….
68      4.157559722
69      3.148745968
70      2.482346774
71      2.836618056
```

7. Submodels

Update calendar
The model timestep is a month.

Update environmental variables
The model takes the temperature and f values of the corresponding month from the input files.

Competition and f

The model calculates the current population density and quantifies the competition effect on food availability (FC, food competition) depending on how far from the carrying capacity (K) the population density (P) is:

If $P < 1.9 * K$, then $FC = (1 - f_{env}) \cdot (1 - \dfrac{P}{2.K - P})$

If $P \geq 1.9 * K$, then $FC = (1 - f_{env}) \cdot (1 - \dfrac{P}{K/10})$

Two equations are used because if $P = 2K$, the first formula gives an error due to a division by 0, and if $P > 2K$, then the formula gives the untrue result of less competition with a bigger population (hence the use of 1.9 as a pivot value).
Competition is only effective if food availability is less than the maximum (hence the use of '$(1 - f)$' in the equation).

Then the model updates the f value in accordance with the quantified food competition:
$f_{eff} = f_{env} + FC$, where f_{env} is the food available in the environment as input into the model from the external files, and f_{eff} the effective food availability.

Proportionally to how much f is lessened compared to the maximum, the size of the current population has an influence on how important the competition is: If the population is below the carrying capacity (K), then food is more available for the present individuals, but if the population is over the carrying capacity, the availability of food is lessened.

Therefore,
if $P > K$, $FC < 0 \Longleftrightarrow f$ decreases
if $P = K$, $FC = 0 \Longleftrightarrow f$ constant
if $P < K$, $FC > 0 \Longleftrightarrow f$ increases

Meaning that the competition is actually calculated depending on how far from the carrying capacity is the population density, and how far from maximum f is the food availability (f_{env}). The less food available and the bigger the population, the higher the competition.
The regulatory effect of this competition lies in the starvation of individuals at lower food availability, which leads to a reduction of the population size with higher competition (combination of low food availability and big population size). f is always contained between 0 and 1.
If the competition is turned off, f is the direct value taken from the input list.

Convert parameters with TC
A temperature correction factor (TC) is calculated using the Arrhenius temperature (TA) and applied to conductance $\dot{v}$, somatic maintenance rate $\dot{k}M$, maturity maintenance rate $\dot{k}M$ and Weibull ageing acceleration $\ddot{h}a$, which are all affected in the same way by the correction factor.
A given metabolic rate X at temperature T is thus modified with:
X(T) = X * exp(TA/Tref - TA/T) with exp(TA/Tref - TA/T) being the correction factor TC, Tref the reference temperature (293.15K), TA = 9000K, and T the actual temperature (in Kelvin) of the organism's life environment.

Change in reserve
The reserve is supplied from ingested food, that is represented in the model by the functional response f (from 0 to 1). Scaled assimilation rate S_A is found with $\dot{p}_A / \{\dot{p}_{Am}\}$, where $\dot{p}_A$ is the assimilation flux (in energy per time) and $\{\dot{p}_{Am}\}$ the maximal assimilation flux per surface area of structure (in energy per time per surface). Since $\dot{p}_A = \{\dot{p}_{Am}\} * f * L^2$, with L the structural length, then $S_A = f * L^2$.

A flux of mobilized energy goes outside of the reserve compartment: the scaled mobilisation flux S_C is the scaled equivalent of $\dot{p}_C$ / $\{\dot{p}_{Am}\}$ therefore equal to:

$L^2 * (g * e / (g + e)) * (1 + L * \dot{k}_M / \dot{v}) = S_C$, where g is the energy investment ratio (the cost of the added volume for this timestep relative to the maximum potentially available energy for growth and maintenance), e is the scaled reserve density (reserve density relative to maximum reserve density) and L the structural length, and with $\dot{k}_M$ the rate of mobilisation of the κ fraction of S_C for somatic maintenance, proportional to structural length, and $\dot{v}$ the energy conductance. The reserve dynamics calculated at each time step correspond to $\partial U_E = S_A - S_C$.

Change in maturity or reproduction buffer
Before puberty (ability to reproduce), changes in maturity level are calculated as the flux of energy going into the maturity compartment, that is the fraction $1-\kappa$ of the mobilisation flux after paying for the maintenance costs of the maturity compartment U_H:

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

The maturity level of the compartment U_H changes each month through the scaled formula for ∂U_H:

$S_R = (1-\kappa) * S_C - \dot{k}_J * U_H = \partial U_H$, when the reproduction buffer U_R does not receive, ∂U_R is set to 0.

Juveniles keep growing until they reach puberty, when the maturity level U_H is equivalent to U_H^p. At this point, they are able to reproduce, thus the energy flux S_R is redirected entirely to the reproduction buffer U_R and the maturity compartment does not increase anymore: U_H is constant and equal to U_H^p. Therefore, after puberty, and except for females undergoing reproduction:

$S_R = (1-\kappa) * S_C - \dot{k}_M * U_H^p = \partial U_R$

Change in structural length
The structural length L is updated thanks to remaining energy of the fraction κ of the mobilisation flux S_C after that somatic maintenance has been paid. The structural length change is equal to $\partial L = (1 / 3) * ((\dot{v}/ g * L^2) * S_C - \dot{k}_M * L)$.

Starvation
When scaled reserve value is below the scaled structural length l value (length relative to maximum length), that is when e < l, it is assumed that the individual is confronted to starving conditions. The kappa rule is altered and as energy is entirely redirected to somatic maintenance and all other fluxes (growth, reproduction or maturation) are set to 0. The model follows these conditions:
Mobilisation flux $S_C = ([\dot{p}_M] / L^3) / \{\dot{p}_{Am}\}$.
Since $[\dot{p}_M] = [E_G] * \dot{k}_M$ and $[E_G] = g * \kappa * \{\dot{p}_{Am}\} /\dot{v}$
we can rewrite $S_C = (L^3 * \dot{k}_M * g * \kappa * \{\dot{p}_{Am}\} /\dot{v}) / \{\dot{p}_{Am}\} = (L^3 * \dot{k}_M * g * kap) / \dot{v}$
then recalculate $\partial U_E = S_A - S_C$.
When e < 0, the organism doesn't have enough energy to pay somatic maintenance and dies.
The starvation strategy used in the population model was chosen among the ones presented in Kooijman (2010) based on Magniez (1983) research on *A. cordatus* reproduction and development.

Ageing
Two ordinary differential equations are calculated: changes in ageing acceleration $\ddot{q}$ (also called the scaled density of damage inducing compounds) and changes in hazard mortality rate $\dot{h}$:

$\partial \ddot{q} = (\ddot{q} * (L / L_m)^3 * s_G + \ddot{h}_a) * e * (\dot{v}/ L - \dot{r}) - \dot{r} * \ddot{q}$
$\partial \dot{h} = \ddot{q} - \dot{r} * \dot{h}$, with $\dot{r} = (3 / L) * \partial L$

These equations are used for the simulation of the accumulation of damage inducing compounds and their effect, following the DEB theory for ageing (Kooijman 2010). Damage inducing compounds density is proportional to reserve mobilisation S_C and influences the hazard mortality rate $\dot{h}$, which is a function of the damage accumulated in the body. Damage inducing compounds are diluted via growth $\dot{r}$, and additionally ageing is calculated with two other parameters, the Weibull ageing acceleration $\ddot{h}_a$ and the Gompertz stress coefficient s_G. In other words, the hazard mortality rate is the simulation of the vulnerability of the individual towards damage, such as the risk of dying from an illness increasing as the individual ages. Additionally, in our model, the ageing submodel relies on a stochastic element, where the individual has a 50% chance of looking into its death probability rate $\dot{h}$.

Update individuals
The calculated changes are applied to each state variables of the individual:

The temporal resolution is a monthly interval: each ODE is calculated then the resulting ∂ is applied * 30.5. For a state variable X, X = X + ∂X * 30.5.

If the individual has reached a maturity level corresponding to a threshold, it updates its life stage (i.e. its breed in NetLogo language) accordingly. The individual also updates its age.

Update reproduction and birth timers

The reproduction calendar (repro_time) and the GSI calendar (GSI_time) advance by one month each timestep, and fall back to the start in a twelve months cycle. The starting date of the two calendars is not the same (March for repro_time and June for GSI_time, see table previously).

The birth timer (birth_time) is only owned by females and is not always running. It is set off if the female has launched reproduction, and it counts down instead of up (e.g. if it was at 7 the month before, the timer will be set to 6 this month). As long as the female has not launched reproduction, the birth timer will stay set at 0. Once the reproduction period starts, the birth timer is what allows to verify if the individual is undergoing reproduction and to adapt its state variables accordingly: at birth_time 8, 7 and 6, females are reproducing (i.e. conceiving offspring by decreasing the energy in their reproduction buffer, see below); at birth_time 3, 2 and 1, females release offspring (i.e. a number of new juveniles proportional to the number of females having reproduced is initiated into the model, see below).

Reproduction

Only females are considered in the reproduction processes. The value of the Gonado-somatic index (GSI = 100 * ((ash-free gonads dry weight) / (ash-free body dry weight)) is increasing monthly until the reproduction period, when the amount of energy accumulated will be checked by the model to allow, or not, the female to participate to reproduction. Whenever the level of GSI reaches at least 0.07%, the female can reproduce, if not, she will continue updating the energy into the reproduction buffer until the next reproduction period.

When females are reproducing, conception of offsprings causes a decrease in energy in their reproduction buffer: their usual ∂U_R is set to 0 for the three months, while U_R is forced to decrease: for each month of the reproduction period the female decreases its buffer by a third of 52% of the energy stored: $\partial_2 U_R = (U_{R\_start} - 0.52 * U_{R\_start}) / 3$,

with U_{R_start} the reproduction buffer at the start of the period (Magniez 1983). The GSI follows a similar pattern (see submodel 'Calculate GSI').

When females release offsprings, five months after conception, 65% of the eggs are assumed to have survived until birth. The reproductive output (Ri) is therefore equal to Ri = 0.65 * eggs For each of the three months of offspring release, the number of juveniles (Ri / 3) are initiated into the model.

Calculate GSI

The GSI is estimated for each month according to the time of accumulation of energy into the reproduction buffer from the end of the reproduction, following the equation:

$$GSI = \frac{time\_of\_accumulation * \dot{k}_M * g}{f^3 * (f + \kappa * g * y_{VE})} * \left((1-\kappa) * f^3 - \frac{\dot{k}_J * U_H^p}{L_m^2 * s_M^3}\right)$$

where the time of accumulation is the number of days since the end of the reproduction period, $\dot{k}_M$ the somatic maintenance rate coefficient and $\dot{k}_J$ the maturity maintenance rate coefficient, g the energy investment ratio, f the scaled functional response, y_{VE} is the parameter for the yield of structure on reserve, that is the number of moles of structure that can be produced with one mole of reserve, s_M the acceleration factor, U_H^p the scaled energy in the complexity compartment at puberty, κ the fraction of energy directed towards structure and 1- κ the fraction of energy directed towards complexity and L_m the maximum volumetric length (see "Entities, State variables and scales" for the dimensions and in-code notations).

The GSI of a reproducing female will decrease by 52% of its initial value over the 3 months period of reproduction (i.e. a decrease of one third of 52% per month):

$\partial GSI = (GSI_{start} - 0.52 * GSI_{start}) / 3$, where GSI_{start} is the level of gonadal index at the onset of reproduction.

Background mortality

The background mortality rate is applied to the overall population: 3.42% of juveniles and 2% of adults (males and females) die each month (calculated from size frequency distribution provided by Mespoulhé 1992). Depending on the cause of death, the individuals set on a certain flag (deceased_bg or deceased_old) and a 'deceased' flag and are removed from the system.

Check temperature
Depending on the temperature for the current and prior month and on the type of sensitivity to temperatures chosen for the model, a mortality rate is applied to the population for temperatures from 8 to 12°C.
For a "vulnerable" setting, temperatures exceeding thresholds of 8, 9.5, 11 and 12°C for two consecutive months cause a mortality rate of 25%, 35%, 45% and 100% respectively. For an "intermediate" setting, temperatures exceeding thresholds of 8, 9.5, 11 and 12°C for only one month cause a mortality rate of 10%, 20%, 30% and 100% respectively.
For a "resistant" setting, temperatures exceeding thresholds of 8, 9.5, 11 and 12°C for two consecutive months cause a mortality rate of 10%, 20%, 30% and 100% respectively.
Population monitoring
At the end of each timestep, population density is calculated and data collected for monitoring and plotting mean values of state variables. Plots are built on the lists compiled out of all individual state variable values.

REFERENCES

•Delille, D., Bouvy, M., 1989. *Bacterial responses to natural organic inputs in a marine subantarctic area*. Hydrobiologia, 182(3), 225-238. doi:10.1007/BF00007517.

•Guillaumot, C., 2019. AmP Abatus cordatus, version 2019/01/17.
https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Abatus_cordatus/Abatus_cordatus_res.html

•Kooijman, S.A.L.M., 2010. *Dynamic energy budget theory for metabolic organisation*, third ed. Cambridge university press.

•Magniez, P. (1983). Reproductive cycle of the brooding echinoid Abatus cordatus (Echinodermata) in Kerguelen (Antarctic Ocean): changes in the organ indices, biochemical composition and caloric content of the gonads. *Marine Biology*, *74*(1), 55-64.

•Martin, B.T., Zimmer, E.I., Grimm, V., Jager, T., 2010. *DEB-IBM User Manual: Dynamic Energy Budget theory meets individual-based modelling: a generic and accessible implementation*. Available at https://www.bio.vu.nl/thb/deb/deblab/debibm/DEB_IBM_manual.pdf.

•Railsback, S.F., Grimm, V., 2019. *Agent-based and Individual-based Modeling: A Practical Introduction*. Princeton university press.

•Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. *The ODD protocol: A review and first update*. Ecological Modelling, 221, 2760-2768. doi: 10.1016/j.ecolmodel.2010.08.019