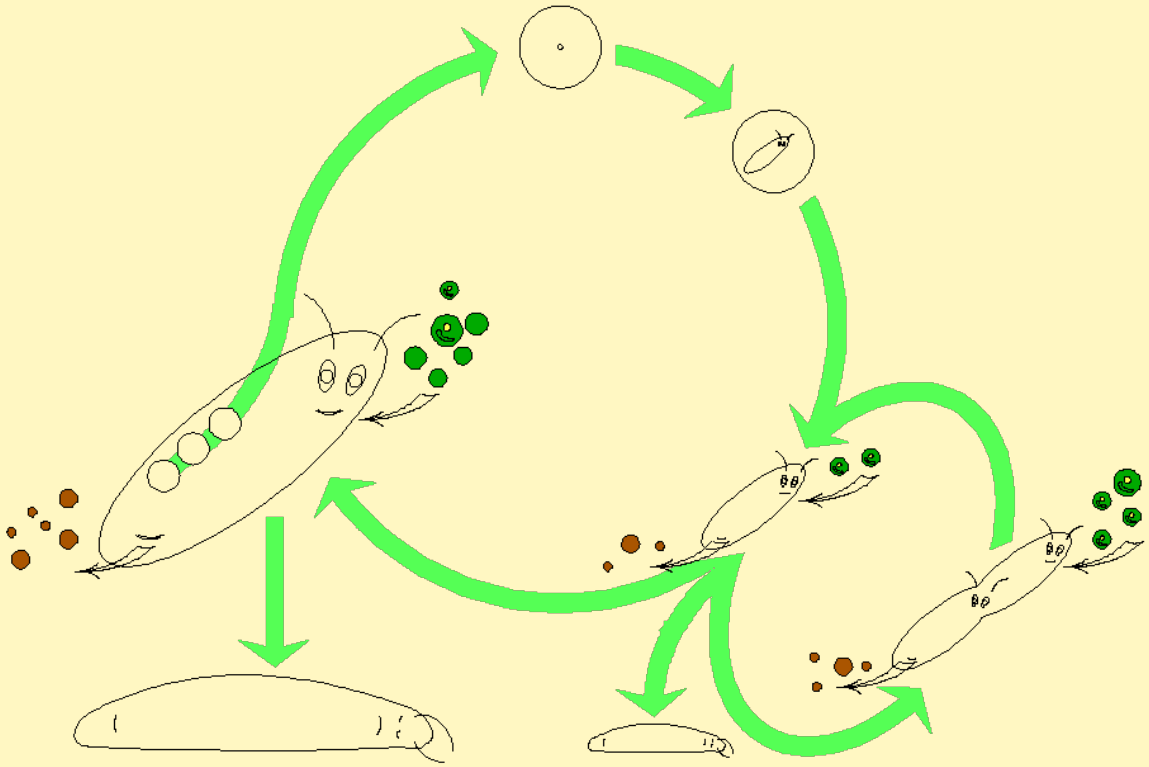
Answers to exercises for

Dynamic Energy Budget tele-course



DEB theory for metabolic organisation

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Chapter 0

Basic methods

These exercises concern the background document Basic methods for Theoretical Biology, which is assumed to be known to participants of the DEB tele-course.

0.1 Dimensions

0.1.1 Answer:

Formally: no problems if $\dim(b) = \sqrt{\text{time}}$ and $\dim(a) = \dim(y)/\sqrt{\text{time}}$. It is unlikely, however, that the model has a (simple) physical interpretation with such dimensions.

0.1.2 Answer:

This model can have a simple physical interpretation if $\dim(c) = \text{time}$ and b is dimensionless, while $\dim(a) = \dim(y)\text{time}^{-1}$. More generally: $\dim(c) = \text{time}\ \dim(d)^2$, which implies $\dim(b) = \text{time}\ \dim(d)^{-1}$, where d has simple but otherwise arbitrary physical dimensions. The fitting of this model to data $\{t_i, y_i\}_{i=1}^n$ yields two parameters only, not three.

If you multiply a and b with a number and divide c by that number, y does not change.

0.2 Scaling of dynamic systems

0.2.1 Answer:

$\dim K = \dim(S)$ because $f = \frac{S}{S+K}$
f is dimensionless because $f = \frac{S}{S+K}$
$\dim(j_S) = \dim(S)/(\text{time}\ \dim(X))$
$\dim(y_{XS}) = \dim(X)/\dim(S)$
$\dim(\dot{r}) = \text{time}^{-1}$

A possible choice for the dimension of S and X is: C-mol . length^{-3}. This does not imply, however, that y_{XS} is necessarily dimensionless; we have $\dim(y_{XS}) = \frac{\text{C-mol X}}{\text{C-mol S}}$ and $\dim(j_S) = \frac{\text{C-mol S}}{\text{time . C-mol X}}$.

0.2.2 Answer:

Five parameters: initial substrate concentration $S(0)$, initial population density $X(0)$, saturation coefficient K, max specific uptake rate j_S, yield coefficient y_{XS}.

0.2.3 Answer:

The scaled system will have $5 - 3 = 2$ parameters, because we can (usually) remove one parameter per variable.

One choice for rescaling is: $s = S/K$, $x = X/(K\, y_{XS})$, $\tau = t\, j_S\, y_{XS}$. The system then becomes

$$\begin{aligned} \frac{d}{d\tau}s &= -fx \\ \frac{d}{d\tau}x &= fx \end{aligned}$$

with $f = \frac{s}{1+s}$ and two parameters: $s(0) = S(0)/K$, $x(0) = X(0)/(K\, y_{XS})$.

0.2.4 Answer:

Since we have no information about $X(t)$, we choose $x = X/(K\, y_{XS})$.

$$\begin{aligned} \frac{d}{dt}S &= -\dot{r}_m K f x \\ \frac{d}{dt}x &= x f \dot{r}_m \end{aligned}$$

with four parameters: $S(0)$, $x(0)$, K, $\dot{r}_m = j_S\, y_{XS}$. The latter parameter has the interpretation of the maximum specific growth rate.

0.2.5 Answer:

Theoretically: yes, because we can estimate $x(0)$ and K, so $y_{XS} = X(0)/(K\, x(0))$. This is remarkable, because we have no direct measurements about the conversion from substrate to biomass. Practically, however, we will see that in presence of a little scatter, the uncertainty in the values for $x(0)$ and K is large, which makes the uncertainty in the value of y_{XS} huge. More elaborate models for biomass growth not necessarily allow to extract the conversion efficiency from these data.

0.3 Theoretical identification of parameter values

0.3.1 Answer:

$\dim(K) = \dim(X)$, because $f = \frac{X}{X+K}$.
f must be dimensionless, because $f = \frac{X}{X+K}$.

$\dim(L_b) = \dim(L) =$ length, because $L(0) = L_b$.
$\dim(L_m) = \dim(L) =$ length, because $L(\infty) = fL_m$, and f is dimensionless.
$\dim(\dot{r}_B) =$ time^{-1}, because $t\dot{r}_B$ must be dimensionless; it occurs as an argument of a transcendental function.
$\dim(\dot{k}_M) = \dim(\dot{r}_B) =$ time^{-1}, because $\dot{r}_B = (3/\dot{k}_M + 3fL_m/\dot{v})^{-1}$.
$\dim(\dot{v}) =$ length/time, because $\dim((fL_m/\dot{v})^{-1}) = \dim(\dot{r}_B) =$ time^{-1}.
g must be dimensionless because $\dim(\frac{\dot{v}}{g\dot{k}_M}) = \dim(L_m) =$ length; $\dim(\dot{v})$ and $\dim(\dot{k}_M)$ are known.

0.3.2 Answer:

Three (compound) parameters only: L_b, fL_m and $\dot{r}_B$.

0.3.3 Answer:

Five parameters are identifiable: L_b, K, $\dot{k}_M$, g and $\dot{v}$. Functions of these parameters, such as f, $\dot{r}_B$ and L_m are identifiable as well, obviously. The relationship between L and t gives information about L_b, $L(\infty)$ and $\dot{r}_B$ (see previous question); the relationship of $L(\infty)$ with X gives information about K and L_m; the relationship between $\dot{r}_B$ with $L(\infty)$ gives information about $\dot{k}_M$ and $\dot{v}$; the relationship between V_m and $\{\dot{v},\ \dot{k}_M,\ g\}$ gives information about g. There might well be *practical* problems with obtaining these parameter values from the two data sets.

0.3.4 Answer:

$\dim(d_V) = \dim(d_E) =$ weight . length^{-3}. Six parameters: $\frac{d_V+f_1d_E}{d_V+f_2d_E}$, K, $(d_V + f_1d_E)V_b$, $V_b/(f_1^3V_m)$, $\dot{k}_M^{-1}+f_1V_m^{1/3}/\dot{v}$, $\dot{k}_M^{-1}+f_2V_m^{1/3}/\dot{v}$. In conclusion we can state that these compound parameters are not very informative.

The parameter $\dot{v}$ is not identifiable, because it has dimension length/ time, but no lengths are measured.

0.3.5 Answer:

Six parameters are identifiable: d_VV_b, d_E/d_V, K, $\dot{k}_M$, g and $d_V^{1/3}\dot{v}$, or functions of these (compound) parameters. Knowledge about the values of X can be used in this case to obtain K and f; this is because the relationship between $W_b = (d_V + fd_E)V_b$ and X has three parameters, K, d_VV_b and d_EV_b, and we have three observations.

0.4 Fitting data

0.4.1 Answer:

After setting the path to debtool/lib, the required code of a script file with the name `exer.m` should read something like this:

```
aL = [0 1; 1 4; 2 5; 3 5.5]; % age-length data

function L = bert(p,aL) % define the von Bert curve
L = p(2) - (p(2) - p(1)) * exp(-p(3) * aL(:,1));
end

p = nrregr('bert', [1 6 1]', aL); % estimate parameters
[cov, cor, sd] = pregr('bert', p, aL); % get standard deviation
[p, sd] % show result
shregr_options('default') % initiate plot settings
shregr('bert', p, aL) % make a plot
```

This should work when you save this script file and run `exer` in the directory where you parked `exer.m`. You can check the correct location by typing `ls`, which should list `exer.m`.

0.5 Inner and outer products

0.5.1 Answer:

Inner product: x'*y. Outer product: x*y'.

0.5.2 Answer:

sum(x.*y). Notice that this equals x'*y.

0.6 Mean and variance

0.6.1 Answer:

Your function can look like this:

function [m, cov, cor] = mcc (x)
[n, k] = size(x);
m = sum(x,1)'/ n;
cov = x' * x/ n - m * m';
sd = diag(cov).^0.5
cor = cov./ (sd * sd');
endfunction

Fill variable x like: x = [1 1.5; 2 1.5; 3 2]
Run your function mcc like: [m, cov, cor] = mcc x
We get

$$m = \begin{pmatrix} 2.00 \\ 1.66 \end{pmatrix} \quad cov = \begin{pmatrix} 0.666 & 0.166 \\ 0.166 & 0.055 \end{pmatrix} \quad cor = \begin{pmatrix} 1.000 & 0.866 \\ 0.866 & 1.000 \end{pmatrix}$$

Notice that this function also works for more than 2 variables.

0.7 Profile likelihood

0.7.1 Answer:

The ln likelihood function for data $\{x_i\}_{i=1}^n$ is $\ell(\lambda) = \ln\lambda \sum_{i=1}^n x_i - n\lambda - \sum_{i=1}^n \ln x_i!$. The ML-estimate is $\hat{\lambda} = \sum_i x_i/n$. The profile ln likelihood function is

$$\ell_p(\lambda) \quad = \quad 2(\ell(\hat{\lambda}) - \ell(\lambda)) = 2n(\lambda - \hat{\lambda}) - 2\ln(\lambda/\hat{\lambda}) \sum_{i=1}^n x_i = 2n\lambda - 2n\hat{\lambda}(1 + \ln(\lambda/\hat{\lambda}))$$

We have to subtract the first term in the second-order Tayler expansion and multiply by 2 to arrive at a function that is comparable with the profile ln likelihood function and obtain

$$\ell_t(\lambda) \quad = \quad (\lambda - \hat{\lambda})^2 \frac{d^2}{d\lambda^2} \ell_(\hat{\lambda}) = (\lambda - \hat{\lambda})^2 \hat{\lambda}^{-2} \sum_i x_i = n(\lambda - \hat{\lambda})^2/\hat{\lambda}$$

The 95% confidence interval is given by

$$\{\lambda | \ell_p(\lambda) < 3.8415\} \quad \text{or} \quad \{\lambda | \ell_t(\lambda) < 3.8415\}$$

Large sample theory has been applied here, so the results only holds for large n. Practice learns, however, that the first confidence interval is close to correct for much smaller values of n than the second interval. The practical problem is that the calculation of the profile likelihood function is generally computationally intensive.

The code can look like this: we create an empty script-file with the name prof.m and write in that file for Octave:

```
x = [3, 2, 4, 3]; % data
n = length(x); % number of data-points
lm = mean(x); % ML estimate for Poisson-parameter
l = linspace(0,3 * lm, 100); % vector of parameter values
f1 = 2 * n * l - 2 * n * lm * (1 + log(l/ lm)); % prof-lik function
f2 = n * (l - lm) .^ 2/ lm; % tangent parabola
plot(l, f1, 'g', l, f2, 'r', ... % plot functions in green and red
[0; 3 * lm], [3.84; 3.84], '6'); % draw line for conf. intervals in black
```

We now run the script-file by typing prof in the Octave comment-line.

0.8 Root finding

0.8.1 Answer:

We first specify the function for which we want to find the root. Your function looks like

```
function f = finda (a)
global x y;
[nx k] = size(x); [ny k] = size(y);
```

```
varx = sum((x(:,2) - a * x(:,1)).^2)/ nx;
vary = sum((y(:,2) - a * y(:,1)).^2)/ ny;
v = x(:,1)' * x(:,2)/varx + y(:,1)' * y(:,2)/ vary;
w = x(:,1)' * x(:,1)/varx + y(:,1)' * y(:,1)/ vary;
f = a - v/w;
end
```

Now we find the root and use your function like:
x = [1 2; 2 2.2; 3 2.3]; y = [2 5; 3 6; 4 6.1]; global x y;
[a, error] = fsolve('finda', 0.1)
[a, error] = fsolve('finda', 2)
Check the value of error to make sure that the numerical procedure converged. It can easily result in nonsense. Notice that the two calls have different results; the one with the highest value for the likelihood function is the proper estimate. Consult Matlabs' manual for fsolve.

Chapter 1

Basic concepts

1.1 Physical versus volumetric length

1.1.1 Answer:

Physical length depends on shape and requires a definition of how the length is taken; volumetric length is independent of shape and represents the cubic root of the physical volume. Both reserve and structure contribute to physical volume; structural length is the cubic root of structural volume. Isomorphy implies that physical length is proportional to volumetric length. Auxiliary theory assumes that a well-chosen physical length is proportional to structural length.

1.2 Temperature correction

1.2.1 Answer:

We should expect a rate of $0.2 \exp(8000/(273 + 20) - 8000/(263 + 37))\,\mathrm{cm\,d^{-1}}$.

1.2.2 Answer:

No, mussels and sparrows don't have the same shape, so a direct comparison of these rates makes no sense. We can remove the effect of shape by turning to volumetric lengths, but we still have the problem that mussels would rapidly die at 40°C, and a sparrow at 20°C. We can infer a theoretical Arrhenius temperature for the sparrow if we know some characteristic rate (such as the energy conductance) for the mussel at 20° and the sparrow at 41°C, and assume that they are the same for both species. This Arrhenius temperature can then be used to make the comparison, given that our assumption holds.

Chapter 2

Standard DEB Model

2.1 Hyperbola

2.1.1 Answer:

Let $h = k = 0$, and $b = a$, so $x^2 - y^2 = a^2$. Introduce $v = x + y$ and $w = x - y$, so $x = (v + w)/2$ and $y = (v - w)/2$. Substitution gives $vw = a^2$. Translate $v = X + K$, $v = 1 - Y$ and set $a^2 = K$, which results in $(1 - Y)(X + K) = K$, or $X = Y(X + K)$, or $Y = (1 + K/X)^{-1}$.

2.2 Homogeneous functions

2.2.1 Answer:

$\frac{\partial z}{\partial x} = ay(t)$ and $\frac{\partial z}{\partial y} = ax(t)$; $\frac{dx}{dt} = b$ and $\frac{dy}{dt} = -c\exp\{-ct\}$, so $\frac{dz}{dt} = ab\exp\{-ct\}(1 - ct)$.

2.2.2 Answer:

1 degree 3

2 degree 1

3 degree 0

4 degree 3

5 degree 3:

6 degree 1:

7 non-homogeneous

8 degree 0:

2.2.3 Answer:

Let $g(t) = f(tx, ty) = t^n f(x, y)$ and introduce $x = tX$ and $y = tY$. Use the chain rule for differentiation to prove that

$$\frac{d}{dt}g(t) = nt^{n-1}f(X,Y) = X\frac{\partial}{\partial x}f(tX,tY) + Y\frac{\partial}{\partial y}f(tX,tY)$$

then let $t = 1$.

2.3 Reserve dynamics

2.3.1 Answer:

Structural mass M_V relates to structural volume V as $M_V = [M_V]V$, where $[M_V]$ is constant due to the assumption of strong homeostasis. So $\dot{r} = M_V^{-1}\frac{d}{dt}M_V = V^{-1}\frac{d}{dt}V$. Structural (volumetric) length L relates to structural volume V as $V = L^3$ by definition. Since $\frac{d}{dt}V = \frac{d}{dt}L^3 = 3L^2\frac{d}{dt}L$, we have $\dot{r} = 3L^{-1}\frac{d}{dt}L$. The change in reserve density is

$$\begin{aligned}
\frac{d}{dt}m_E &= M_V^{-1}\frac{d}{dt}M_E - \dot{r}m_E \\
&= j_{EA} - M_V^{-1}M_E(\frac{\dot{v}}{L} - \dot{r}) - \dot{r}m_E \quad \text{for } j_{EA} = \dot{J}_{EA}/M_V \\
&= j_{EA} - m_E\frac{\dot{v}}{L}
\end{aligned}$$

No change in reserve density occurs if $m_E = j_{EA}L/\dot{v}$. It remains constant during growth (of juveniles and adults) if $j_{EA} \propto L$ and the proportionality factor is constant. This holds if $\dot{J}_{EA} \propto L^2$ and food density remains constant. DEB theory assumes that $\dot{J}_{EA} = f\{\dot{J}_{EAm}\}L^2$, where the scaled functional response is a function of food density, with a maximum of 1 and the proportionality factor $\{\dot{J}_{EAm}\}$ is constant. Reserve density in juveniles and adults is at maximum at steady state if assimilation is at maximum; For $M_V = [M_V]L^3$ it then has value $m_{Em} = \frac{j_{EAm}L}{\dot{v}} = \frac{\dot{J}_{EAm}L}{M_V\dot{v}} = \frac{\{\dot{J}_{EAm}\}L^3}{[M_V]L^3\dot{v}} = \frac{\{\dot{J}_{EAm}\}}{[M_V]\dot{v}}$. Weak homeostasis means that the chemical composition of the whole body (reserve and structure) remain constant during growth at constant food density. This reserve dynamics as function of the states of the individual (amounts of reserve and structure) is the only one that satisfies this condition. The assumptions behind this reserve dynamics are

1 food is first converted to reserve that is mobilised

2 the mobilisation rate only depends on the state of the individual: amounts of reserve and structure

3 reserve and structure obey strong homeostasis

4 the individual is isomorphic

5 weak homeostasis applies

The difference with first order dynamics is in the dilution by growth. First order dynamics would result in $\dot{J}_{EC} = M_E \frac{\dot{v}}{L}$ rather than $\dot{J}_{EC} = M_E(\frac{\dot{v}}{L} - \dot{r})$. Since the DEB reserve dynamics uniquely follows from assumption 1-5, first order dynamics is not weakly homeostatic, even if assumptions 1-4 apply. The mean residence time of a molecule in reserve is $\frac{M_E}{\dot{J}_{EC}} = \frac{M_E}{M_E(\frac{\dot{v}}{L} - \dot{r})} = (\frac{\dot{v}}{L} - \dot{r})^{-1}$. Notice that is time decreases with increasing length.

2.4 Maximum growth

2.4.1 Answer:

At constant food, length changes as $\frac{d}{dt}L = \dot{r}_B(L_\infty - L)$, so $\frac{d^2}{dt^2}L = -\dot{r}_B^2(L_\infty - L)$. Since the latter continuously decreases, growth in length is maximal at birth, so $L = L_b$.

Weight is proportional to cubed length, and cubed length changes as $\frac{d}{dt}L^3 = 3L^2\frac{d}{dt}L = 3L^2\dot{r}_B(L_\infty - L)$ and $\frac{d^2}{dt^2}L^3 = 3\dot{r}_B^2(L_\infty - L)(2L_\infty - 3L)$. The latter equals zero if $L = \frac{2}{3}L_\infty$, so growth in weight is maximal at $L = \max(L_b, \frac{2}{3}L_\infty)$.

Relative growth of length is maximal if $\frac{d}{dt}\left(L^{-1}\frac{d}{dt}L\right) = 0$, i.e. if $L\frac{d^2}{dt^2}L = \left(\frac{d}{dt}L\right)^2$. Substitution shows that the equation has no meaningful solution, while the relative growth in length only decreases. This implies that it is maximal at birth.

Relative growth of weight is maximal if $\frac{d}{dt}\left(L^{-3}\frac{d}{dt}L^3\right) = 0$, which leads to the same result as for relative growth of length.

Notice that growth of length and weight behave quite differently, but relative growth of length and weight are behave quite similar.

2.5 Numerical behaviour of growth and reproduction

2.5.1 Answer:

Observe that lengths and reproduction satiate monotoneously to an asymptotic value for isomorphs at constant food, while weight-curves are sigmoidal, because they relate to cubed length. Also observe that organisms do not complete the juvenile stage at low food levels.

2.6 Reserve buffer for reproduction

2.6.1 Answer:

Allocation to reproduction is in continuous time, so allocation per time increment is incrementally small only, not sufficient to produce an embryo. Buffer handling rule can span a wide spectrum:

- some rotifers produce on egg after the other.

- waterfleas produce eggs clutch-wise, coupled to the moulting cycle.
- mussels spawn once a year, coupled to the season.
- albatrosses nest every other year.
- bamboo trees set seed once every seven or so years.

Chapter 3

Energy, compounds and metabolism

3.1 Body mass and composition

3.1.1 Answer:

If we exclude contributions from the reproduction buffer to weight for simplicity's sake, the relationship between mass in gram and C-mole is for $* = E, V$

$$\begin{aligned} W_d &= w_E M_E + w_V M_V; \quad w_* = 12n_{C*} + 1n_{H*} + 16n_{O*} + 14n_{N*} \\ W_w &= w_E^w M_E + w_V^w M_V; \quad w_*^w = 12n_{C*} + 1n_{H*}^w + 16n_{O*}^w + 14n_{N*} \end{aligned}$$

where $n_{CE} = n_{CV} = 1$ per definition (of C-mole) and $n_{HE}^w = n_{HE} + 2x_E$, $n_{OE}^w = n_{OE} + x_E$, $n_{HV}^w = n_{HV} + 2x_V$, $n_{OV}^w = n_{OV} + x_V$. So $w_E + 18x_E = w_E^w$ and $w_V + 18x_V = w_V^w$. Notice that water does not affect the quantification of mass in C-moles (M_E and M_V), only the molecular weights (w_E and w_V). The question is to specify the moles of water per carbon in reserve and structure, x_E and x_V. The values of x_E and x_V must be found from

$$\begin{aligned} 0 &= 10W_d - W_w \quad \text{which was given} \\ 0 &= 10(w_E M_E + w_V M_V) - w_E^w M_E - w_V^w M_V \\ 0 &= (10w_E - w_E^w)m_E + 10w_V - w_V^w \\ 0 &= (9w_E - 18x_E)m_E + 9w_V - 18x_V \end{aligned}$$

As implied from what was given, the ratio of dry weight W_d and wet weight W_w (both in gram) does not seem to depend on the ratio $m_E = M_E/M_V$ of mass of reserve M_E and mass of structure M_V (both in C-mole). Our result shows that this is only possible if the molecular weights of dry reserve and structure are equal, $w_E = w_V$ and the fraction of water in reserve and structure must be equal, $x_E = x_V = x$. The implication is $x = w_V/2 = w_E/2$. So for $n_{HE} = n_{HV} = 1.8$, $n_{OE} = n_{OV} = 0.5$ and $n_{NE} = n_{NV} = 0.2$, we have for dry mass $w_E = w_V = 24.6\,\mathrm{g/mol}$, $x = 12.3\,\mathrm{g/mol}$ and the chemical indices for wet mass are $n_{HE}^w = n_{HV}^w = 1.8 + 2 \times 12.3 = 26.4$ and $n_{OE}^w = n_{OV}^w = 0.5 + 12.3 = 12.8$. The resulting molecular weight for wet mass is $w_E^w = w_V^w = 12{+}1{\times}26.4{+}16{\times}12.8{+}14{\times}0.2 = 246\,\mathrm{g\,mol^{-1}}$, which checks the result. Our result also shows that a constant (so nutrition independent) ratio between wet and dry weight can only be an approximation at best.

3.1.2 Answer:

The definition of the fraction of energy in ingested food that is fixed in reserve is $\kappa_X = \dot{p}_A/\dot{p}_X$. The definition of the yield coefficient of reserve on food is $y_{EX} = \dot{J}_{EA}/\dot{J}_{XA}$. The relationship between energy and mass fluxes for food and reserve is $\dot{p}_X = \dot{J}_{XA}\mu_X$ and $\dot{p}_A = \dot{J}_{EA}\mu_E$, respectively. So $\kappa_X = \frac{\dot{J}_{EA}\mu_E}{\dot{J}_{XA}\mu_X} = y_{EX}\mu_E/\mu_X$. Notice that κ_X is really dimensionless, but the units of y_{EX} are a mole of E per mole of X; y_{EX} is not really dimensionless because E and X are different types.

3.1.3 Answer:

In the context of the standard DEB model, carbon in food can end up in reserve, faeces and carbon dioxide. The conservation of carbon implies $1 = y_{CX} + y_{PX} + y_{EX}$. The yield of carbon dioxide on food is given by $y_{CX} = 1 - y_{PX} - y_{EX}$. If $y_{EX} = 1$, we must have $y_{CX} = y_{PX} = 0$.

3.2 Metabolic transformation

3.2.1 Answer:

Section 4.3.1 on metabolic transformation applies Section 3.5 on macrochemical transformation. The three transformations are for $Y^A_{XX} = Y^G_{EE} = Y^D_{EE} = 1$:

assimilation A**:** $Y^A_{XX}\,\mathrm{X} + Y^A_{OX}\,\mathrm{O} \to Y^A_{EX}\,\mathrm{E} + Y^A_{PX}\,\mathrm{P} + Y^A_{CX}\,\mathrm{C} + Y^A_{HX}\,\mathrm{H} + Y^A_{NX}\,\mathrm{N}$

growth G**:** $Y^G_{EE}\,\mathrm{E} + Y^G_{OE}\,\mathrm{O} \to Y^G_{VE}\,\mathrm{V} + Y^G_{CE}\,\mathrm{C} + Y^G_{HE}\,\mathrm{H} + Y^G_{NE}\,\mathrm{N}$

dissipation D**:** $Y^D_{EE}\,\mathrm{E} + Y^D_{OE}\,\mathrm{O} \to Y^D_{CE}\,\mathrm{C} + Y^D_{HE}\,\mathrm{H} + Y^D_{NE}\,\mathrm{N}$

Since assimilation is the only process that involves Y^A_{EX} or Y^A_{PX}, the superscript A is suppressed; a similar reason applies to superscript G for Y^G_{VE}. Moreover Y is replaced by $-y$ in these cases to express that the yield coefficients are constant and to make y positive. Eq (3.12) can be applied to find the yield coefficients. For assimilation we have for the chemical element C, H O and N in the rows with $y_{XX} = 1$:

$$\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 1.8 & 0 \\ 0.5 & 2 \\ 0.2 & 0 \end{pmatrix} \begin{pmatrix} -y_{XX} \\ Y^A_{OX} \end{pmatrix} + \begin{pmatrix} 1 & 1 & 1 & 0 & 0 \\ 2 & 1.8 & 0 & 2 & 3 \\ 0.5 & 0.5 & 2 & 1 & 0 \\ 0.15 & 0.15 & 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} y_{EX} \\ y_{PX} \\ Y^A_{CX} \\ Y^A_{HX} \\ Y^A_{NX} \end{pmatrix}$$

This can be rearranged to separate known from unknown

$$\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 2 & 0 & 3 \\ 2 & 1 & 2 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} Y^A_{CX} \\ Y^A_{HX} \\ Y^A_{OX} \\ Y^A_{NX} \end{pmatrix} = - \begin{pmatrix} 1 & 1 & 1 \\ 1.8 & 2 & 1.8 \\ 0.5 & 0.5 & 0.5 \\ 0.2 & 0.15 & 0.15 \end{pmatrix} \begin{pmatrix} -y_{XX} \\ y_{EX} \\ y_{PX} \end{pmatrix}$$

and solved

$$\begin{pmatrix} Y^A_{CX} \\ Y^A_{HX} \\ Y^A_{OX} \\ Y^A_{NX} \end{pmatrix} = -\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 2 & 0 & 3 \\ 2 & 1 & 2 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}^{-1} \begin{pmatrix} 1 & 1 & 1 \\ 1.8 & 2 & 1.8 \\ 0.5 & 0.5 & 0.5 \\ 0.2 & 0.15 & 0.15 \end{pmatrix} \begin{pmatrix} -1 \\ y_{EX} \\ y_{PX} \end{pmatrix} = -\begin{pmatrix} 1 & 1 & 1 \\ 0.6 & 0.775 & .675 \\ -1.05 & -1.138 & -1.088 \\ 0.2 & 0.15 & 0.15 \end{pmatrix} \begin{pmatrix} -1 \\ y_{EX} \\ y_{PX} \end{pmatrix}$$

The same can be done for growth for $y_{EE} = 1$ with the results

$$\begin{pmatrix} Y^G_{CE} \\ Y^G_{HE} \\ Y^G_{OE} \\ Y^G_{NE} \end{pmatrix} = -\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 2 & 0 & 3 \\ 2 & 1 & 2 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}^{-1} \begin{pmatrix} 1 & 1 \\ 2 & 1.8 \\ 0.5 & 0.5 \\ 0.15 & 0.15 \end{pmatrix} \begin{pmatrix} -y_{EE} \\ y_{VE} \end{pmatrix} = -\begin{pmatrix} 1 & 1 \\ 0.775 & 0.675 \\ -1.24 & -1.09 \\ 0.15 & 0.15 \end{pmatrix} \begin{pmatrix} -1 \\ y_{VE} \end{pmatrix}$$

And for dissipation

$$\begin{pmatrix} Y^D_{CE} \\ Y^D_{HE} \\ Y^D_{OE} \\ Y^D_{NE} \end{pmatrix} = -\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 2 & 0 & 3 \\ 2 & 1 & 2 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}^{-1} \begin{pmatrix} 1 \\ 2 \\ 0.5 \\ 0.15 \end{pmatrix} \begin{pmatrix} -y_{EE} \end{pmatrix} = \begin{pmatrix} 1 \\ 0.775 \\ -1.137 \\ 0.15 \end{pmatrix}$$

The assumptions that we used are

- the basic structure of the standard DEB model (food is first converted to reserve that is mobilised for other transformations)
- strong homeostasis (the chemical indices are fixed)
- dioxygen is a substrate that is non-limiting (Chapter 5 deals with multiple substrates)

Notice that reproduction is only represented in the form of overhead costs as part of the dissipation flux. From a chemical point of view reserve of the mother is 'transformed' into reserve of the offspring, which has the same composition.

The yields relate to the fluxes as $Y^A_{EX} = \dot{J}_{EA}/\dot{J}_{XA} = -y_{EX}$ and $Y^A_{VE} = \dot{J}_{VG}/\dot{J}_{EG} = -y_{VE}$. The dissipation flux collects all fluxes that represent the mineralisation of reserve; this includes somatic and maturity maintenance, maturation and overhead of reproduction.

The yield coefficients have units $\dim(y_{EX}) = \frac{\text{mol } E}{\text{mol } X}$ and $\dim(y_{VE}) = \frac{\text{mol } V}{\text{mol } E}$. Although the difference is subtle, the yield coefficients are not dimensionless, since X, E and V represent different types.

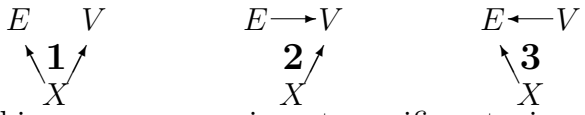
The relationships between mass and energy fluxes are $\dot{p}_X = \mu_X \dot{J}_{XA}$, $\dot{p}_A = \mu_E \dot{J}_{EA}$, $\dot{p}_G = \mu_E \dot{J}_{EG}$ and $\dot{p}_D = \mu_E \dot{J}_{ED}$, were μ_X and μ_E are the chemical potentials of food and reserve, respectively. The flux $\dot{p}_G$ represents the flux allocated to growth, while $\kappa_G \dot{p}_G = \mu_V \dot{J}_{VG}$ is the flux fixed in new structure. So $y_{VE} = \frac{\dot{J}_{VG}}{\dot{J}_{EG}} = \frac{\kappa_G \dot{p}_G/\mu_V}{\dot{p}_G/\mu_E} = \frac{\kappa_G \mu_E}{\mu_V}$.

The total flux of dioxygen is $\dot{J}_O = Y^A_{OX}\dot{p}_X/\mu_X + Y^D_{OD}\dot{p}_D/\mu_E + Y^G_{OG}\dot{p}_G/\mu_E$.

3.2.2 Answer:

The situation in standard DEB model with its two pools is much simpler: food is transformed to reserve and reserve to structure. While food density might fluctuate wildly, growth changes smoothly are a result of the buffering capacity of the reserve pool. Now this buffering does not exist. What are the implications?

The four possible transformations are $X \to y_{EX}E$, $X \to y_{VX}V$, $E \to y_{VE}V$ and $V \to y_{EV}E$, suppressing all mineral substrates and products. We have here $y_{VE} \neq y_{EV}^{-1}$ and the values must be such that possibly limiting mineral compounds (such as ammonia) are always products, never substrates. (Dioxygen is a typically substrate under aerobic conditions, but is supposed to be non-limiting; facultative fermentation is discussed Chapter 4.) This also applies to the standard DEB model, but we now have 4 transformations, not 2. The interconversion of E and V causes a non-uniqueness that must but eliminated, somehow, for instance by assuming that for each time increment we have one of three possible cases:



Suppose that biomass was growing at specific rate $\dot{r}_0 = \dot{r}(t)$ at t, so $\frac{d}{dt}M_W(t,\dot{r}_0) = \dot{r}_0 M_W(t,\dot{r}_0)$, with $M_W(t,\dot{r}_0) = M_V(t)\,(1 + m_E(\dot{r}_0))$ and $m_E(\dot{r})$ is some known smooth function of $\dot{r}$. To make it more concrete for $m_E = \frac{e\{\dot{j}_{EAm}\}}{\dot{v}[M_V]}$ (see Table 3.3), the standard DEB model assumes $e = g\frac{\dot{k}_M(1+L_T/L)+\dot{r}}{\dot{v}/L-\dot{r}}$ (Eq (2.21)), so $m_E(\dot{r})$ is monotonically increasing (for $\dot{r} < \dot{v}/L$, which is always the case). This can only be linked to the intake rate if the scaled functional response is constant for sufficiently long period; the difference with the present situation is that this link is direct, and $m_E(\dot{r})$ might be a different function.

The amount of food that is transformed in the infinitesimally small time interval $(t, t+dt)$ is $M_X(t) = \dot{J}_{XA}(t)\,dt$, where $\dot{J}_{XA}(t)$ might fluctuate wildly, including a white-noise process. This food is converted to biomass at some unknown specific rate $\dot{r}_1 = \dot{r}(t+dt)$, so $M_W(t+dt,\dot{r}_1) = M_V(t+dt)\,(1 + m_E(\dot{r}_1))$, where we need to find $\dot{r}_1 = (M_W(t+dt,\dot{r}_1)/M_W(t,\dot{r}_0) - 1)\,/dt$. Given m_E and $\dot{r}_o$ and M_E and M_V at t such that $M_E/M_V = m_E(\dot{r}_0)$, we need to solve $\dot{r}_1$ and so θ in one of three cases

Case 1: $$\frac{M_E + \theta y_{EX} M_X}{M_V + (1-\theta) y_{VX} M_X} = m_E(\dot{r}_1) \quad \text{with } \dot{r}_1 = \dot{J}_{XA}\frac{\theta y_{EX} + (1-\theta) y_{VX}}{M_E + M_V}$$

Case 2: $$\frac{M_E - \theta M_E}{M_V + y_{VX} M_X + \theta y_{VE} M_E} = m_E(\dot{r}_1) \quad \text{with } \dot{r}_1 = \frac{y_{VX}\dot{J}_{XA} + (y_{VE}-1)\theta M_E/dt}{M_E + M_V}$$

Case 3: $$\frac{M_E + y_{EX} M_X + \theta y_{EV} M_V}{M_V - \theta M_V} = m_E(\dot{r}_1) \quad \text{with } \dot{r}_1 = \frac{y_{EX}\dot{J}_{XA} + (y_{EV}-1)\theta M_V/dt}{M_E + M_V}$$

Case 1 applies if a solution for θ exists between 0 and 1. If not, case 2 applies if $\dot{r}_1 < \dot{r}_0$ and $\frac{d}{d\dot{r}}m_E(\dot{r}_1) > 0$ or $\dot{r}_1 > \dot{r}_0$ and $\frac{d}{d\dot{r}}m_E(\dot{r}_1) < 0$. Otherwise case 3 applies.

The problem we have to study is that a sudden change in food density $X(t)$ translates into a sudden change in ingestion rate $\dot{J}_{XA}$ and so in growth rate $\dot{r}_1$ and biomass composition $m_E(\dot{r}_1)$. In the cases 2 and 3, θ is not necessarily small (so θ/dt can be large), so that a

possibly large fraction of one generalized compound needs to be transformed into the other and in the next incrementally small time interval it might be reversed. These backward and forward transformations represent not only an energy (and mineral) loss, but it might be physically impossible to do this within a time increment. Stochasticity in the feeding rate directly translates into stochasticity in the composition. Animals are organisms that feed on other organisms. If food organisms would also follow this rule, food would have a stochastic composition, which translates into a stochastic conversion efficiency. So apart from being physically impossible, the construct also becomes hopelessly complex in situations where food availability is erratic. The discrete nature of food particles also causes problems of a related nature, since nothing is smoothing the transitions. The conclusion is that working with a variable composition in absence of a smoothing buffer is asking for problems and the only way to avoid these problems is to partition biomass into pools of constant composition.

3.3 Enzyme kinetics

3.3.1 Answer:

The RU then resembles enzyme kinetics better for increasing $\dot{k}_A$ and $\dot{k}_B$, the SU for decreasing values. This relates directly to the way RU and SU are obtained as limiting cases of enzyme kinetics.

3.3.2 Answer:

The maximum relative difference is about 0.25, which is reached for $n_A = n_B \to \infty$ and $\dot{J}_A = \dot{J}_B \to 0$; under these conditions the impact is maximal of the waiting time of the other compound. The relative difference is not much in many practical cases (i.e. low values for n_A and n_B), which is important because we frequently do not know the absolute stoichiometry.

3.3.3 Answer:

Yes; we can decrease the amount of time that transformations have to be delayed because the SU has to wait for the last-arriving substrate by increasing the number of copies of substrate and that of product.

3.3.4 Answer:

The relative differences in binding fractions can be considerable; the substrate-SU complex is relative more abundant than the substrate-RU or substrate-enzyme complexes, because the dissociation rates for SUs is zero.

3.3.5 Answer:

The end-result is a mix of enzyme, product in concentration $X_C = \min(X_A/n_A, X_B/n_B)$ and substrate A in the concentration $X_A - n_A X_C$ or substrate B in concentration $X_B - n_B X_C$; one of the substrates completely disappeared.

If substrate i, for $i \in \{A, B\}$, is left over, and the other substrate hardly limited the transformation, the initial appearence rate of product C is $\dot{J}_C = J_{Cm}/(1 + X_i^{-1}\dot{k}_C/\dot{b}_i)$. The rate is almost constant, most of the time, but later drops gradually, depending on the parameter values. If this applies, we can solve the waiting time t till the practical end of the transformation from $t\dot{J}_C = n_i X_i$, which gives $t = n_i(X_i + \dot{k}_C/\dot{b}_i)/\dot{J}_{Cm}$. This is an underestimation, because the transformation slows down, and the other substrate could have been co-limiting. The latter can be taken into account in a rough way, by $t = n_i(X_i + \dot{k}_C/\min(\dot{b}_i, \dot{b}_j))/\dot{J}_{Cm}$. This still represents an underestimation.

3.3.6 Answer:

For the sequential-substitutable case we have for $\boldsymbol{\theta} = \begin{pmatrix} \theta_{..} & \theta_{A\cdot} & \theta_{\cdot B} & \theta_{AB} \end{pmatrix}^T$

$$\begin{aligned}
\frac{d}{dt}\theta_{..} &= \dot{k}_A\theta_{A\cdot} + \dot{k}_B\theta_{\cdot B} - (\rho_A\dot{J}_A + \rho_B\dot{J}_B)\theta_{..} \\
\frac{d}{dt}\theta_{A\cdot} &= \rho_A\dot{J}_A\theta_{..} - \dot{k}_A\theta_{A\cdot} \\
\frac{d}{dt}\theta_{\cdot B} &= \rho_B\dot{J}_B\theta_{..} - \dot{k}_B\theta_{\cdot B} \\
\frac{d}{dt}\theta_{AB} &= 0 \quad \text{so} \\
\frac{d}{dt}\boldsymbol{\theta} &= \dot{\boldsymbol{k}}_{ss}\boldsymbol{\theta} \quad \text{with} \quad \dot{\boldsymbol{k}}_{ss} = \begin{pmatrix} -\rho_A\dot{J}_A - \rho_B\dot{J}_B & \dot{k}_A & \dot{k}_B & 0 \\ \rho_A\dot{J}_A & -\dot{k}_A & 0 & 0 \\ \rho_B\dot{J}_B & 0 & -\dot{k}_B & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}
\end{aligned}$$

For the sequential-complementary case

$$\begin{aligned}
\frac{d}{dt}\theta_{..} &= \dot{k}_C\theta_{AB} - \rho_A\dot{J}_A\theta_{..} \\
\frac{d}{dt}\theta_{A\cdot} &= \rho_A\dot{J}_A\theta_{..} - \rho_B\dot{J}_B\theta_{A\cdot} \\
\frac{d}{dt}\theta_{\cdot B} &= 0 \\
\frac{d}{dt}\theta_{AB} &= \rho_B\dot{J}_B\theta_{A\cdot} - \dot{k}_C\theta_{AB} \quad \text{so} \\
\frac{d}{dt}\boldsymbol{\theta} &= \dot{\boldsymbol{k}}_{sc}\boldsymbol{\theta} \quad \text{with} \quad \dot{\boldsymbol{k}}_{sc} = \begin{pmatrix} -\rho_A\dot{J}_A & 0 & 0 & \dot{k}_C \\ \rho_A\dot{J}_A & -\rho_B\dot{J}_B & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & \rho_B\dot{J}_B & 0 & -\dot{k}_C \end{pmatrix}
\end{aligned}$$

For the parallel-substitutable case

$$\begin{aligned}
\frac{d}{dt}\theta_{\cdot\cdot} &= \dot{k}_A\theta_{A\cdot} + \dot{k}_B\theta_{\cdot B} - (\rho_A\dot{J}_A + \rho_B\dot{J}_B)\theta_{\cdot\cdot} \\
\frac{d}{dt}\theta_{A\cdot} &= \rho_A\dot{J}_A\theta_{\cdot\cdot} + \dot{k}_B\theta_{AB} - \rho_B\dot{J}_B\theta_{A\cdot} - \dot{k}_A\theta_{A\cdot} \\
\frac{d}{dt}\theta_{\cdot B} &= \rho_B\dot{J}_B\theta_{\cdot\cdot} + \dot{k}_A\theta_{AB} - \rho_A\dot{J}_A\theta_{\cdot B} - \dot{k}_B\theta_{\cdot B} \\
\frac{d}{dt}\theta_{AB} &= \rho_B\dot{J}_B\theta_{A\cdot} + \rho_A\dot{J}_A\theta_{\cdot B} - \dot{k}_A\theta_{AB} - \dot{k}_B\theta_{AB} \quad \text{so} \\
\frac{d}{dt}\boldsymbol{\theta} &= \dot{\boldsymbol{k}}_{ps}\boldsymbol{\theta} \quad \text{with} \quad \dot{\boldsymbol{k}}_{ps} = \begin{pmatrix} -\rho_A\dot{J}_A - \rho_B\dot{J}_B & \dot{k}_A & \dot{k}_B & 0 \\ \rho_A\dot{J}_A & -\rho_B\dot{J}_B - \dot{k}_A & 0 & \dot{k}_B \\ \rho_B\dot{J}_B & 0 & -\rho_A\dot{J}_A - \dot{k}_B & \dot{k}_A \\ 0 & \rho_B\dot{J}_B & \rho_A\dot{J}_A & -\dot{k}_A - \dot{k}_B \end{pmatrix}
\end{aligned}$$

For the parallel-complementary case

$$\begin{aligned}
\frac{d}{dt}\theta_{\cdot\cdot} &= \dot{k}_C\theta_{AB} - (\rho_A\dot{J}_A + \rho_B\dot{J}_B)\theta_{\cdot\cdot} \\
\frac{d}{dt}\theta_{A\cdot} &= \rho_A\dot{J}_A\theta_{\cdot\cdot} - \rho_B\dot{J}_B\theta_{A\cdot} \\
\frac{d}{dt}\theta_{\cdot B} &= \rho_B\dot{J}_B\theta_{\cdot\cdot} - \rho_A\dot{J}_A\theta_{\cdot B} \\
\frac{d}{dt}\theta_{AB} &= \rho_A\dot{J}_A\theta_{\cdot B} + \rho_B\dot{J}_B\theta_{A\cdot} - \dot{k}_C\theta_{AB} \quad \text{so} \\
\frac{d}{dt}\boldsymbol{\theta} &= \dot{\boldsymbol{k}}_{pc}\boldsymbol{\theta} \quad \text{with} \quad \dot{\boldsymbol{k}}_{pc} = \begin{pmatrix} -\rho_A\dot{J}_A - \rho_B\dot{J}_B & 0 & 0 & \dot{k}_C \\ \rho_A\dot{J}_A & -\rho_B\dot{J}_B & 0 & 0 \\ \rho_B\dot{J}_B & 0 & -\rho_A\dot{J}_A & 0 \\ 0 & \rho_B\dot{J}_B & \rho_A\dot{J}_A & -\dot{k}_C \end{pmatrix}
\end{aligned}$$

Chapter 4

Univariate DEB models

4.1 Wood production

4.1.1 Answer:

Volume V grows as $\frac{d}{dt}V = 0.1\frac{d}{dt}L\,\mathrm{m}^3/\mathrm{a}$, and diameter L_D grows in a ways that can easily be expressed in terms of L.

4.1.2 Answer:

Since wood production ceases, if we believe Preston et al, wood production cannot be associated with assimilation and dissipation, because these processes do not cease. It must therefore be associated with growth only. Other data, however, suggest that wood production continues if the tree is already fully grown.

4.2 Carbon dioxide production

4.2.1 Answer:

The carbon dioxide flux cannot be zero if $y_{EX} < 1$, because the anabolic component of assimilation is than *producing* carbon dioxide, and no other process is fixing it. The condition is, however, more stringent. The specific substrate flux is $j_{XA} = f j_{XAm}$, the specific maintenance flux of reserve is $j_{EM} = y_{EV}\,\dot{k}_M$ and that for growth is $j_{EG} = y_{EV}\,\dot{r} = y_{EV}\frac{f-l_d}{f+g}\dot{k}_E$, with $y_{EV} = y_{VE}^{-1}$ and $l_d = g\dot{k}_M/\dot{k}_E$. So the carbon dioxide flux is zero if

$$y_{VE}(y_{EX} - 1) f j_{XAm} = \dot{k}_M + (1 - y_{VE})\dot{k}_E \frac{f - l_d}{f + g}$$

or

$$0 = (y_{EX} - 1) j_{XAm} f^2 + \left(g(y_{EX} - 1) j_{XAm} - \dot{k}_M y_{EV} - (y_{VE} - 1)\dot{k}_E\right) f + (y_{EV} - 1)\dot{k}_M$$

This can be summarized by $0 = af^2 + bf + c$. The scaled functional response f can be solved from this quadratic equation in f. A positive real solution for f exists if $y_{EX} > 1$,

and $0 < f < 1$ if $\sqrt{b^2 - 4ac} - b > 2a$, or $-c < b + a$. A zero carbon dioxide flux is possible for some substrate density if

$$(1 + g)(y_{EX} - 1)j_{XAm} + (1 - y_{VE})\dot{k}_E > \dot{k}_M$$

Some text books mention that for each produced carbon dioxide molecule, two methane molecules have been consumed by a methanotroph. This exercise shows, however, that such a fixed relationship does not exist; it is very sensitive for environmental conditions.

Methane burning in assimilations' catabolic component should generate enough energy to drive assimilations' anabolic component. So $\mu_X j^C_{XA} > (\mu_E - \mu_X)j^A_{XA}$ or $\mu_X(1 - y_{EX}) > (\mu_E - \mu_X)y_{EX}$ or $y_{EX} > \mu_E/\mu_X$.

Notice that, like carbon dioxide, ammonia is taken up as well as excreted. We know apriori that ammonium uptake always exceeds excretion at steady state.

4.3 Numerical behaviour of fluxes and states

4.3.1 Answer:

Initially embryos have a negligibly small structure, which implies that the structure-specific fluxes are very large. Weights include reserve and structure. The initial amount of reserve is substantial, so weight-specific fluxes are not blown up. Embryos get more reserve from the mother than juveniles can possibly obtain by eating. This is why embryos can grow faster than juveniles on a relative basis.

4.3.2 Answer:

You will see that if the elemental compositions of reserve and structure do not differ a lot, the respiration ratio stays more or less constant. This explains why respiration ratios are usually taken to be constant in experimental animal physiology. You can also see that if the composition differ substantially, the respiration ratio varies a lot with size. This explains why respiration ratios are usually not taken to be constant in microbiology.

4.3.3 Answer:

The comment for section 4.3.3 explains the evaluation.

4.4 Practical identification of parameter values

4.4.1 Answer:

The constraint on the maintenance rate coefficients implies that stage transitions occur at fixed amounts of structure. We need (compound) DEB parameters first, which are independent of food availability, and then use these to obtain the quantities of interest. Start Octave, set the path to DEBtool/animal and type `p = [1; 1; 5; 7; 0.01]; [q,`

`U] = get_pars_g(p)` . The result $U_E = 7.195$, $1.6606\,\mathrm{d.cm^2}$ represents the scaled reserve at age 0 and a_b, so the fraction of reserve that is left over at birth is $1.66/7.195 = 0.23$. We now type `[r, U] = iget_pars_g(.7,q)` . The result $U_E = 6.7707$, 1.1624 d.cm^2 shows that the fraction of reserve that is left over at birth now equals $1.16/6.77 = 0.17$, and that the ultimate length is r(3) = 3.5 cm, the age at birth r(4) = 7.4 d, and the von Bertalanffy growth rate r(5) = $0.0108\,\mathrm{d}^{-1}$. Notice that the von Bertalannfy growth rate is now higher, and the ultimate length lower than at abundant food, but the growth curves at different food levels do not intersect. The effect of the reduced food availability on the fraction of reserve that is left over at birth is relatively large because the reserve density at birth drops from 1 till 0.7, and because a lower initial reserve increases the age at birth, and so the cumulative maintenance costs.

4.4.2 Answer:

Type `get_pars_r([1; 1; 3; 5; 7; 0.01; 0.7])` and find the answer $\kappa = 0.729$. This estimate depends on the length at puberty because of the maturity maintenance costs are competing with allocation to reproduction.

4.4.3 Answer:

Type `[q, U] = get_pars_s([1 0.7; 4.4 4.4; 10.2 10.1; 25 17.5; 0.03 0.042; 2.6 1]')` . The answer is: $\kappa = 0.81$, $g = 0.21$, $\dot{k}_J = 0.36\,\mathrm{d}^{-1}$, $\dot{k}_M = 0.54\,\mathrm{d}^{-1}$, $\dot{v} = 2.8$ cm/d, $M_H^b/\{\dot{J}_{EAm}\} = 1.46\,\mathrm{d\,cm^2}$ and $M_H^p/\{\dot{J}_{EAm}\} = 20.7\,\mathrm{d\,cm^2}$.

The fractions of reserve that are left over at birth is $30.46/41.65 = 0.73$ for $f = 1$ and $21.14/32.57 = 0.65$ for $f = 0.7$. The ages at birth are $a_b = 5.1$ d for $f = 1$ and 5.2 d, respectively.

All values that have cm in their units depend on length. these are $\dot{v}$, $M_H^b/\{\dot{J}_{EAm}\}$ and $M_H^p/\{\dot{J}_{EAm}\}$.

4.5 Parameter estimation

4.5.1 Answer:

If the temperature is constant, rate parameters are constant. Living in the thermal neutral zone means no energy is required to maintain a constant body temperature (at $37^/circ$C), so $\{\dot{p}_T\} = 0$. The von Bertalannfy growth rate is $\dot{r}_B = \frac{\dot{k}_M/3}{1+f/g}$, see Eq. (2.24), and the energy investment ratio is $g = \frac{\dot{v}[M_V]}{\kappa\{\dot{J}_{EAm}y_{VE}} = \frac{\dot{v}d_V y_{EV}}{\kappa w_V\{\dot{p}_{Am}\mu_E}$, see Table 3.3.

Chapter 5

Multivariate DEB models

5.1 Simultaneous nutrient limitation

5.1.1 Answer:

You will see large effects for small throughput rates. When you think of a community as a more complex chemostat, this observation should motivate you to include nutrient recycling in all basic community models.

5.1.2 Answer:

We can expect this for non-limiting reserves that are hardly excreted.

5.2 Plant physiology

5.2.1 Answer:

You will see that for proper combinations of parameter values plants' allocation to roots versus shoots partly compensates adverse effects on growth rates, despite the fact that such a response is not incorporated explictly in the DEB model.

5.2.2 Answer:

You will see that for proper combinations of parameter values a peak in shoots' reserve density occurs during a short period, just after germination. Notice that the occurrence of this behaviour has not been incorporated explicitly in the DEB model; it is a consequence of how roots and shoots exchange metabolites. This, however, does not exclude the existence of regulation mechanisms for the growth and absorption of cotyledons.

5.3 Kidney size and function

5.3.1 Answer:

The flux of nitrogen waste can be written as $\dot{J}_N = \eta_{NA}\dot{p}_A + \eta_{ND}\dot{p}_D + \eta_{NG}\dot{p}_G$ (cf page 147 of the DEB book). All powers $\dot{p}_*$ are cubic polynomials in (scaled) length (cf page 123). This means that nitrogen waste production can be written as a cubic polynomial in (scaled) length

$$\dot{J}_N = \dot{J}_{N3}l^3 + \dot{J}_{N2}l^2 + \dot{J}_{N1}l + \dot{J}_{N0}$$

The coefficients $\dot{J}_{N*}$ can be obtained by straightforward substitution in the expressions given at page 123 where we take $e = 1$.

A reasonable approximation for the cortex volume is $V_c = \delta\,(L^3 - (L - L_c)^3)$, where δ is a dimensionless coefficient that takes care of the kidney shape, L is a typical length measure of the kidney, and L_c is the thickness of the cortex.

If cortex thickness L_c would be proportional to kidney length L, cortex volume would be proportional to L^3, and so proportional to body volume. Since nitrogen waste production is a weighted sum of squared and cubed length, this would imply that the work load of the cortex tissue decreases with body size.

Let us now allow more complex relationships between cortex thickness and kidney length, and linearize this function: $L_c(L) = L_{c0} + \delta_c L$. Obviously we must have $L > L_{c0}$, and we assume that the kidney is not functional for smaller body sizes. The cortex volume now amounts for $\delta_m = 1 - \delta_c$ to

$$V_c = \delta\left((1 - \delta_m^3)L^3 + 3\delta_m^2 L_{c0}L^2 - 3\delta_m L_{c0}^2 L + L_{c0}^3\right)$$

The workload of cortex tissue remains constant during development if

$$\begin{aligned}
\dot{J}_{N3} &= \dot{J}_{Nr}(1 - \delta_m^3) \\
\dot{J}_{N2} &= 3\dot{J}_{Nr}\delta_m^2 L_{c0}/L_0 \\
\dot{J}_{N1} &= -3\dot{J}_{Nr}\delta_m L_{c0}^2/L_0^2 \\
\dot{J}_{N0} &= \dot{J}_{Nr}L_{c0}^3/L_0^3
\end{aligned}$$

Where $\dot{J}_{Nr}$ is a reference flux, and L_0 a reference length. These 4 equations determine $\dot{J}_{Nr}$, L_0, $\delta_c = 1 - \delta_m$ and L_{c0} as function of parameters of the DEB.

Chapter 6

Effects of compounds on budgets

6.1 Ageing

6.1.1 Answer:

The DEB module has 2 ageing parameters: the ageing acceleration $\ddot{h}_a$ and the Gompertz stress coefficient s_G. If the growth period is short, these two parameters can be reformulated in the Weibull and Gompertz ageing rates, $\dot{h}_W$ and $\dot{h}_G$. Both the Weibull and the Gompertz ageing models also have 2 parameters. The general Gompertz model and the Weibull model with shape parameter 3 are special cases of the DEB module, but because of the larger shape plasticity of the DEB module, the general Weibull model can be approximated very well, see Section 6.1.1 of the comments on 'Empirical Weibull curves'. Part of this larger plasticity is due to the energetics module of the DEB model; the Weibull and the Gompertz models don't have such a coupling. Only if tissue differentiation is irreversible and if other causes of death play a minor role, species are affected by ageing (as an effect if free radicals).

6.2 Toxicokinetics

6.2.1 Answer:

See DEBtool/tox/mydata_acc. The result is an elimination rate of $0.9\,\mathrm{d}^{-1}$, and a BCF of $4.88\,\mathrm{l/g}$. The standard deviations are very large.

6.2.2 Answer:

See DEBtool/tox/mydata_acceli. The result is an elimination rate of $0.58\,\mathrm{d}^{-1}$, and a BCF of $5.47\,\mathrm{l/g}$. The standard deviations are still large, but much smaller than for accumulation data only. Notice that the fit for the accumulation phase is less good, because the elimination phase suggest different parameter values.

6.2.3 Answer:

Because the size of the animals differed, it is likely that the BCF is constant, but the elimination rates differ, so we choose for the parametrization $C(t) = K(1 - \exp\{-\dot{k}_e t\}$.

We now write a script file where we fill the data, define the regression functions, estimate the parameters and obtain the standard deviations.

```
tc1 = [0 1 2 3 4 5; 0, 3.1 5.9 8.1 9.  9.5]';
tc2 = [0 1 2 3 4 5; 0, 2.9, 5.7, 7.9 8.9 9.4]';
function f = myacc0(p,tc)
K = p(1); ke = p(2);
f = K*(1-exp(-tc(:,1)*ke));
end
p0 = nrregr("myacc0",[10 .3]',[tc1;tc2]);
ssq0 = ssq("myacc0",p0,[tc1;tc2]);
function [f1,f2] = myacc1(p,tc1,tc2)
K = p(1); ke1 = p(2); ke2 = p(3);
f1 = K*(1-exp(-tc1(:,1)*ke1));
f2 = K*(1-exp(-tc2(:,1)*ke2));
end
p1 = nrregr("myacc1",[15 .3 .3]', tc1, tc2);
ssq1 = ssq("myacc1",p1, tc1, tc2);
6 * log(ssq0/ssq1)
```

The result is 0.414, which is not significant at the 5 % level, because under the null hypothese this represents a random trial from a Chi-square distribution with 1 degree of freedom.

6.3 Concentration-Survival relationships

6.3.1 Answer:

Type `t = [0 1]'; c = [0 1 2 4 8 16]';`

```
S = [10 10 10 10 10 10; 10 9 10 8 4 1];
p = nmsurv2(''fomort'', [.02 1.5 .6 1]',t,c,S);
p = nmsurv2(''fomort'', p, t, c, S);
lc50(p([2 3 4]),1);
```

The elimination rate walks to large values in this example, which explains the convergence problems. The standard deviation of the NEC can only be obtained here by fixing the elimination rate. The standard deviations appear after:

```
[cov, cor, sd] = psurv2(''formort'', [p, [1 1 1 0]'], t, c, S); [p, sd]
```

The result is NEC = 2.9 (sd 1.1) mg/l, the LC50.1d = 6.9 mg/l.

6.3.2 Answer:

Without any recalculation we know that the blank mortality rate , the killing rate and the elimination rate is two times as small. This follows directly from a change in time-units.

6.3.3 Answer:

The NEC will be multiplied by the factor x, and the killing rate will be divided by that factor.

6.3.4 Answer:

Type `t = [0 1 2 3 4 5]'; c = 5; S = [100 69 17 3 0 0]'; p = scsurv2('fomort', [1e-8 1.5 .6 1; 0 1 1 1]', t, c, S); lc50(p([2 3 4],1),t)`

The result is NEC = 0.73 mM, the LC50 for day 1 2 3 4 5 is 7.2, 2.9, 1.9, 1.5, 1.3 mM.

6.4 Extrapolation from acute to chronic LC50 values

6.4.1 Answer:

Set 1 has the lowest ultimate LC50, because the LC50 for set 1 decreases more between day 2 and 3.

6.4.2 Answer:

Type:

```
tc1 = [1 2 3; 23.5 8 4.5]';
tc2 = [1 2 3; 23.5 7.9 4.5]';
p1 = lc503(tc1, [.5 1 .1]);
lc50(p1,4); p2 = lc503(tc2,p1); lc50(p2,4);
```

The LC50.4d appears because the output of lc50 is not assigned to a variable. The ultimate LC50's equal the NEC, which are in `p1(1)` and `p2(1)`, respectively. They appear by typing: `[p1, p2]` . This can be checked by typing:

```
lc50(p1,1e8); lc50(p2,1e8)
```

The values are 0.362 and 0.748 mg/l.

Notice that the small difference between the LC50.2d for the two sets, results in a factor 2 difference in the NEC. This illustrates the unstability of extrapolation while the LC50 is still decreasing.

6.4.3 Answer:

Type: `shregr(''lc50'',p1,tc1)` . The mean squared deviation is zero, because three LC50 values exactly determine three parameter values.

6.4.4 Answer:

Type: `tc=[tc1;4 3]; p=nrregr(‘‘lc50’’,p1,tc); lc50(p,[5 6]);`
The answer is LC50.5d = 2.25 mg/l and LC50.6d = 1.78 mg/l.

The graphical check is done by typing:
`shregr_options(‘‘default’’); shregr(‘‘lc50’’,p,tc);`
The fit should by quite good, but the mean squared deviation is not longer zero.

6.5 Extrapolation of effects from one compound to that of another

6.5.1 Answer:

The ratio of the P_{ow} values for compound 2 and 1 is $10^8/10^7 = 10$. The toxicity parameters for compound 2 are: NEC = 1/10 mM, killing rate = 10 $\mathrm{mM}^{-1}\,\mathrm{d}^{-1}$ and the elimination rate = $0.01/\sqrt{10}\,\mathrm{d}^{-1}$. The LC50.2d is found from DEBtool/tox/lc50, by typing: `lc50([0.1, 10, 0.01/sqrt(10)],2)`
The result is 35.63 mM. The LC50.2d for compound 1 is 113.27 mM.

6.6 Effects of pH on toxicity

6.6.1 Answer:

Type:
```
t = [0 1 2 3 4]';
cph = [0 2 4 8 16; 7.8 7.7 7.4 7.0 6.5]';
S = [10 10 10 10 10; 10 10 10 10 8; 10 10 10 8 4; 10 10 9 6 1; 10 9 6 3 0];
p = [1e-8 0.1 4 .2 0.5 1 8.0; 0 1 1 1 1 1 0]';
q = nmsurv2("fomortph",p,t,cph,S);
p = scsurv2("fomortph",q,t,cph,S);
```

The routine nmsurv2 does not come to full conversion, but that is not necessary to get scsurv2 converged. The calculations lead to NECS of 0.00665 and 0.00678 mM for the molecular and ionic forms. Notice that the number of estimated parameters is rather large relative to the available information from data. This implies substantial uncertainty in the values. Check this with the standard deviations.

6.7 Effects on reproduction

6.7.1 Answer:

The result is

mode of action	NEC	EC50.21 d	EC50.∞ d
assimiliation	1.61	2.72	2.58
maintenance costs	1.38	2.75	2.20
growth costs	$*$	2.95	2.82
reproduction costs	0.50	2.50	0.81
neonate survival	1.38	2.51	1.82

$*$: Effects via growth resulted in slow kinetics, with a NEC-time of 11.72 mM d.
The NEC differ by a factor 3 for the various modes of action.

6.8 Interpolation methods for sublethal effects

6.8.1 Answer:

If the change in body length is always of the log-logistic type, it amounts to:

$$\frac{d}{dt}\ln L(c,t) \;=\; \frac{d}{dt}\ln L_{0,t} - \beta_t \frac{\left(\frac{d}{dt}\ln\beta_t\right)\ln\frac{c}{c_{e,t}} - \frac{d}{dt}\ln c_{e,t}}{1+(c_{e,t}/c)^{\beta_t}}$$

The first observation is that relative growth at any given concentrations is that in the blank minus something that depends on concentration and exposure time.

Since it is very probable that $\frac{d}{dt}c_{e,t} < 0$ and $\frac{d}{dt}\beta_t > 0$, growth at any given concentration ceases before that in the blank. Suppose that shrinking can be excluded. While $\frac{d}{dt}L(c,t) = 0$, we must have that

$$\frac{d}{dt}\ln L_{0,t} = \beta_t \frac{\left(\frac{d}{dt}\ln\beta_t\right)\ln\frac{c}{c_{e,t}} - \frac{d}{dt}\ln c_{e,t}}{1+(c_{e,t}/c)^{\beta_t}}$$

We here see an unpleasant implication: the change in the EC50 and the slope depends on the behaviour in the blank. This line of thought should be worked out in further detail. The aim of this exercise has been to show that fitting a sigmoid curve to length data comes with implicit assumptions of the growth process.

6.8.2 Answer:

We find that for $\dot{R}(c,t) = \frac{d}{dt}N(c,t)$ and $\dot{R}_{0,t} = \frac{d}{dt}N_{0,t}$, and $N_{0,t} = N_{0,t_0} + (t-t_0)\dot{R}_0$ for some appropriate value for t_0 (after which the reproduction in the blank is constant):

$$\frac{d}{dt}\ln N(c,t) \;=\; \frac{d}{dt}\ln N_{0,t} - \beta_t \frac{\left(\frac{d}{dt}\ln\beta_t\right)\ln\frac{c}{c_{e,t}} - \frac{d}{dt}\ln c_{e,t}}{1+(c_{e,t}/c)^{\beta_t}}$$

$$\frac{\dot{R}(c,t)}{N(c,t)} = \frac{\dot{R}_0}{N_{0,t_0}+(t-t_0)\dot{R}_0} - \beta_t \frac{\left(\frac{d}{dt}\ln\beta_t\right)\ln\frac{c}{c_{e,t}} - \frac{d}{dt}\ln c_{e,t}}{1+(c_{e,t}/c)^{\beta_t}}$$

Suppose that some exposure time exists after which the reproduction rate at concentration c remains constant, so $N(c,t) = N_{c,t_0} + (t-t_0)R_c$. The slope and the EC50 can then also no longer change ($\frac{d}{dt}\beta_t = 0$ and $\frac{d}{dt}c_{e,t} = 0$), because the slope and the EC50 would become functions of N_{0,t_0}, while they should be independent of what happens in the blanc. So the second term disappears, and the equation applies for all t, which results in $N_{c,t_0}/\dot{R}_c = N_{0,t_0}/\dot{R}_0$. This result cannot hold, because it depends on an arbitrary choice for t_0.

Generally, the concentration-response curve at 22 d cannot be of the log-logistic type if that at 21 d is of the log-logistic type. This devalidates the routine application of this response curve in cases like this, and all the statistics that comes after the assumption that this model would be correct. The present derivation rests on the existence of moments in time after which the reproduction rate does not change. This is consistent with empirical data; this line of thought might be generalized to relax this condition. For the time being, again the conclusion must be that fitting a sigmoid curve to the cumulative number of offspring per female comes with far reaching implicit assumptions about the reproduction process. In this case it might well be that the result can only imply non-sense.

6.9 Effects on populations

6.9.1 Answer:

The result is

mode of action	NEC	EC50.2d	EC50.∞d	unit
init mort	2.85	4.34	4.34	mM
mort.	2.98	4.31	2.99	mM
growth rate	3.39	4.21	3.41	mM

Notice that the EC50 does not depend on time if the compound affects initial mortality only. The NECs differ just a little, the EC50.2d even less; the EC50.∞d is more sensitive to the mode of action. The goodness of fit is excellent in all cases.

6.9.2 Answer:

Population growth is assumed to be exponential in the blank, although this cannot be checked in the present numerical example. The living populations are always growing exponentially at all modes of action, but the measurements include dead cells. This means that the measured populations deviate from exponential growth if the effects are on mortality and initial mortality. The population growth rate (of the living population) equals that in the blank for effects on initial mortality.

Chapter 7

Extensions of DEB models

7.1 Responses to starvation

7.1.1 Answer:

The reponses can be ranked as follows

-1 Migration to avoid (predictable) starvation.

0 No response; the reserve will decrease according to the same rules as during feeding. Growth will cease at a certain reserve density threshold; reproduction continues.

1 Allocation to maturity maintenance and reproduction is ceased at a certain reserve density threshold; this threshold is decreased to the no-growth threshold.

2 Structure is degraded to pay somatic maintenance costs.

3 Somatic maintenance is reduced by ceasing activety (dormancy) and allocation to heating (in endotherms).

4 Suicide reproduction or spore formation. The individual sacrifices itself for the benefit of its progeny.

7.2 Stomach dynamics

7.2.1 Answer:

The waiting time is $t = -[M_{sm}]V^{1/3} \ln \alpha / \{\dot{J}_{Xm}\}$.

7.2.2 Answer:

Gut residence time is also proportional to length.

7.2.3 Answer:

The ratio of the waiting times for stomach emptying of mother and baby is $(4/64)^{1/3} = 2.5$, which implies that the baby has to eat $2.5 \times 3 = 7.5$ times a day to experience the same fluctuations. It is because the baby takes milk, and the mother less nutritial food, that the baby can do with a lower frequency.

Chapter 8

Co-variation of parameters

8.1 Identification of primary parameters

8.1.1 Answer:

$K = \{\dot{J}_{XAm}\}/\{\dot{F}_m\}$ is a compound parameter, but $\{\dot{J}_{XAm}\} = \{\dot{J}_{EAm}\}/y_{EX}$ is that as well, like $E_m = \{\dot{J}_{EAm}\}/\dot{v}$. Since y_{EX} is basic to the biochemical machinery, which all eukaryotes share, it must a primary parameter and is intensive. $\{\dot{J}_{EAm}\}$ is preferred above $\{\dot{J}_{XAm}\}$ as primary parameter, because it is evolutionarily easier to change the feeding capacity than the assimilation capacity. Moreover, it is more close to the maximum length, which depends on maintenance. The searching rate $\{\dot{F}_m\}$ is close to the underlying processes, compared with the half-saturation coefficient K and is an intensive parameter. The energy conductance has a direct relationship with the mechanism of reserve mobilisation, so it is chosen to be a primary parameter, and is intensive. Moreover the maximum reserve capacity shares the property with the maximum length as being a ratio of incomming and outgoing fluxes; both ratios are compound parameters. With the choice of $\{\dot{F}_m\}$, y_{EX}, $\{\dot{J}_{EAm}\}$, $\dot{v}$ as primary parameter and K, $\{\dot{J}_{XAm}\}$, E_m as compound parameters, only one primary parameter is a design parameter, the rest is intensive.

8.2 Scaling relationships

8.2.1 Answer:

1) All parameters can be classified as intensive or design parameters.
2) Simply functions of design parameters are intensive.
3) Maximum length is a function of only one design parameter.

8.2.2 Answer:

1) Effects per molecule inside the individual don't depend of the partition coefficient.
2) Toxico-kinetics is quantified by the one-compartment model (or extensions of it)

3) This model is based on fugacity, which implies a skew symmetry for the roles of both media.

8.3 Effect of changes in parameter values

8.3.1 Answer:

If you decrease κ, investment to reproduction increases, but this does not necessarily translate into more offspring. This is because food uptake is coupled to size, and so to growth, and offspring has to be produced from food (via reserves). An increase maintenance has many consequences for scaling relationships and size control.

Chapter 9

Living together

9.1 Chemostat dynamics

9.1.1 Answer:

You will see that biomass density is at maximum in absence of maintenance, while it is zero in presence of maintenance. The rate at which biomass density increases as a function of very small troughput rates depend on the specific maintenance costs.

9.1.2 Answer:

Product density can be a rather complex function of throughput rate if the coupling coefficients to assimilation and growth become negative.

9.1.3 Answer:

The substrate balance in the chemostat is

$$\frac{d}{dt}X = (X_r - X)\dot{h} - \frac{X j_{XAm}}{X+K} X_V$$

which gives $X_V^* = \frac{(X_r - X)(X+K)\dot{h}}{X j_{XAm}}$ at steady state. The specific growth rate equals the throughput rate at steady state, so $\dot{r}^* = \frac{f^* \dot{k}_E - g\dot{k}_M}{f^* + g} = \dot{h}$. So $f^* \equiv \frac{X^*}{X^*+K} = g\frac{\dot{k}_M + h}{\dot{k}_E - h}$ and $X = K\frac{f}{1-f}$. Product formation (see page 148 of the DEB book) equals: $j_P = \zeta_{PM}\dot{k}_M g + \zeta_{PA}\dot{k}_E f^* + \zeta_{PG} g\dot{h}$. The product balance in the chemostat is

$$\frac{d}{dt}X_P = X_V j_P - X_P \dot{h}$$

so that the steady state product concentration is $X_P^* = X_V^* j_P / \dot{h}$. This completes the biological part. Reactor's design parameters are the reactor volume V, the substrate concentration in the feed X_r and the throughput rate $\dot{h}$.

The balance equation for the financial costs is simple: The total money flux is

$$\dot{S} = \$_P \dot{J}_P - \$_X \dot{J}_X - \$_V \dot{J}_V$$

where $\$_*$ represents the mole-specific financial costs, and the molar product flux $\dot{J}_P = \dot{h} V X_P^*$, the molar substrate flux in the feed $\dot{J}_X = \dot{h} V X_r$, and the biomass flux $\dot{J}_V = \dot{h} V X_V^*$.

We now maximize S as function of the design parameters of the reactor. Since the money flux is linear in the reactor volume, the latter cannot be optimised yet. A realistic inclusion of the financial costs for stirring and cooling into the money flux can define the optimal size of the reactor.

This scheme can be made more realistic by including costs for labour and maintenance of the reactor, climate control, marketing, processing of substrate and medium in the effluent, or regeneration costs for the medium, for instance. Some costs, such as costs for transportation and for the medium, can be included in the coefficients $\$_*$ as long as they are linear in the amounts.

The next step is to code the money flux and maximise is numerically given estimates of the parameter values. This is not difficult in Octave or Matlab.

This application illustrates the typical situation that the DEB theory has to be supplemented with application-specific components to arrive at practical results.

9.1.4 Answer:

Since the chemostat is dwelled by V1-morphs, their total biomass can be conceived of as a single individual. The unusual elements are that this 'super' V1-morph grows without becoming bigger, because the chemostat has a drain, and that the growth rate is human-controlled rather that the result of physiological processes that can be manipulated in an indirect way only.

9.2 Alga-grazer systems

9.2.1 Answer:

It is possible to find combinations of parameter values for which the grazer hardly benefits (i.e. becomes more abundant) from grazing: it is killing the "chicken with the golden eggs". It is also possible to find parameter combinations for which the prey/predator ratio is rather insensitive to changes in substrate, which corresponds with a weak homeostasis situation. This marks the transition to a symbiontic system that can be captured with a single structural component.

Chapter 10

Evolution

10.1 Homeostasis

10.1.1 Answer:

The primary function of reserve is to incorporate metabolic memory. Bacteria live off many substrate, which they take up from the environment independently, while animals live off other organisms that already have all substrates that they need.

10.2 Reorganisation

10.2.1 Answer:

Partitionning, and especially merging, occurred frequently as part of the process of coupling and uncoupling of reserves, so increasing and decreasing the number of reserves, such that the overall dynamics is not affected. Organisational simplicity of integrated units is a functional constraint for robustness and regulatory systems.

10.3 Evolutionary memory

10.3.1 Answer:

The earliest mammals were carnivores, which explains why feeding on plants was rather problematic and the conversion efficiency from grass to cow is that low. The chemical composition of plants and animals differ more than within animals. Increasing the number of reserves was not an option (for several reasons). Quite a few plant taxa are not green and can't, therefore use photons as energy substrate. The earliest eukaryotes where heterotrophic; plants acquired phototrophy by symbiogenesis, but without refraining from heterotrophy. To mention another example: All plants and animals have mitochondria, which they acquired by symbiogenesis.

Chapter 11

Evaluation

11.1 Empirical evidence

11.1.1 Answer:

The explanations are given in Tables 11.2 and 11.3 of the comments.

11.2 Production versus assimilation models

11.2.1 Answer:

SfG models typically ignore the embryo stage and subtract respiration from assimilation before considering production. Maintenance is typically identified with respiration (but not in DEB theory). Explicitly or not, growth overheads are typically included in respiration, which points to a fundamental problem in SfG-models. They also have problems to combine weak homeostasis with reserve, see Section 11.3 of the comments on topological alternatives.