Individual DEB-based structured population modeling

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Main aim

Use of DEB theory for modelling of individuals (lecture Bas Kooijman) and use for modelling population model, including Add-my-Pet collection code and parameter values

Case study to illustrate the approach

Allows for comparative studies of population dynamics between species including population feedback on resources and predation by predators

In communities or ecosystems species differ only in DEB parameters values

Outline

- Dynamic Energy Budget individual model
- Formulation of Cohort Projection Model (CPM)
- Case study electric ray fish *Torpedo marmorata* population
- Constant or periodical environment
- Predator (structured) – prey (unstructured) model

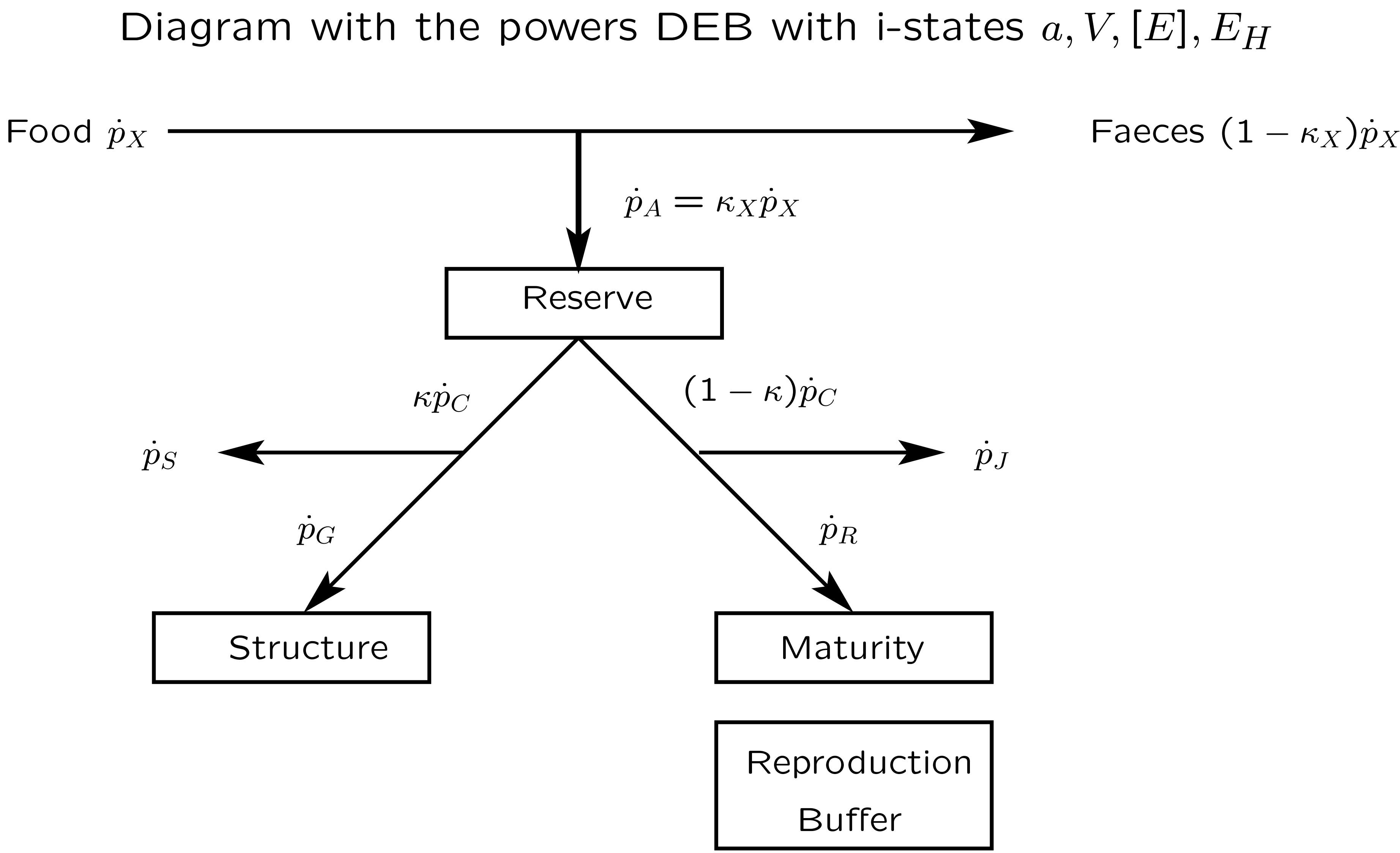
Diagram with the powers DEB with i-states $a, V, [E], E_H$
Food $\dot{p}_X$
Faeces $(1-\kappa_X)\dot{p}_X$
$\dot{p}_A = \kappa_X \dot{p}_X$
Reserve
$\kappa \dot{p}_C$
$(1-\kappa)\dot{p}_C$
$\dot{p}_S$
$\dot{p}_J$
$\dot{p}_G$
$\dot{p}_R$
Structure
Maturity
Reproduction
Buffer

Three stages

$0 \leq a \leq a_b$	embryonic:	no feeding	no reproduction
$a_b \leq a \leq a_p$	juvenile:	feeding	no reproduction
$a_p \leq a \leq n$	adult:	feeding	reproduction

Individual variables:

a: age
V: Structural volume
$[E]$: Reserve density
E_H: Energy allocated to maturity

Population variables:

t: time
X: food density
N: population density

DEB-individual model a: age t: time

$$\left\{ \frac{dV}{da} = \frac{\kappa(\{\dot{p}_{Am}\}/[E_m])[E]V^{2/3} - \dot{k}_M[E_G]V}{\kappa[E]+[E_G]}, \quad E_H^0 \le E_H \right.$$

$$\left\{ \begin{array}{ll} \frac{d[E]}{da} = -\{\dot{p}_{Am}\}V^{-1/3}[E]/[E_m] \,, & E_H^0 \le E_H < E_H^b \\ \frac{d[E]}{da} = \{\dot{p}_{Am}\}V^{-1/3}\Big(f(X(t)) - [E]/[E_m]\Big) \,, & E_H^b \le E_H^p \end{array} \right.$$

$$\left\{ \begin{array}{ll} \frac{dE_H}{da} = (1-\kappa)\Big(\{\dot{p}_{Am}\}\frac{[E]}{[E_m]}V^{2/3} - [E]\frac{dV}{da}\Big) - \dot{k}_J E_H \,, & E_H^0 \le E_H < E_H^p \\ \frac{dE_R}{da} = 0 \,, & E_H^0 \le E_H < E_H^p \\ \frac{dE_H}{da} = 0 \,, & E_H^p \le E_H \\ \frac{dE_R}{da} = (1-\kappa)\Big(\{\dot{p}_{Am}\}\frac{[E]}{[E_m]}V^{2/3} - [E]\frac{dV}{da}\Big) - \dot{k}_J E_H^p \,, & E_H^p \le E_H \end{array} \right.$$

$f(X(t))$: forcing function (food)

Interaction with food X

Scaled Holling type II functional response:

$$f(X(t)) = \frac{X(t)}{X_k + X(t)}$$

Functional response $F(t)$:

$$F(X(t)) = \begin{cases} 0 & \text{if} \quad E_H \leq E_H^b \\ \{\dot{p}_{Xm}\}\frac{X(t)}{X_k+X(t)}V^{2/3} & \text{if} \quad E_H \geq E_H^b \end{cases},$$

where X_k is the half-saturation constant and we use the fact that embryo's do not feed.

Reproduction

Sex ratio is assumed to be 1:1

and male and female eggs/foetuses are equally costly; only females directly contribute to the production of off-spring. Reproduction efficiency only aspects the conversion of the contents of the reproduction buffer to off-spring, so the idea is that half of it is 'lost' for the production of males.

Reproduction is Periodical, Synchronous and Iteroparous

No post-reproductive period

Multiple reproductive cycles over the course of its lifetime occurs for all individuals at years $j = 0 \ldots$

Examples: fish populations as a specific short period of the year with spawning related to mating success but also by food availability for the offspring

Conditions at fertilisation

Two issues related to Initial conditions at fertilisation not discussed here

1. Property of Von Bertalanffy model

2. Energy reserves are densities and defined $[E] = E/V$

Von Bertalanffy model

Von Bertalanffy individual growth model

$$\frac{dV}{dt} = \alpha V^{2/3} - \beta V \qquad V(0) = V_0$$

The solution initial value problem

$$V(t)^{1/3} = \frac{\alpha}{\beta} + (V_0^{1/3} - \frac{\alpha}{\beta})e^{-\beta/3\, t}$$

with $\lim_{t\to\infty} V(t)^{1/3} = \alpha/\beta$

We introduce the two new parameters r_B and L_∞

$$L(t) = V(t)^{1/3}\,, \quad r_B = \frac{\beta}{3}\,, \quad L_\infty = \frac{\alpha}{\beta}$$

then

$$L(t) = L_\infty - (L_\infty - L_0)e^{-r_B\, t}$$

Explanation Von Bertalanffy model for small initial value

$$\frac{dL^3}{dt} = \alpha L^2 - \beta L^3 = 3L^2 \frac{dL}{dt}$$

$L(0) = V(0) = 0$ gives $V(t) = 0$

or dividing by L^2 gives

$$3\frac{dL}{dt} = \alpha - \beta L$$
$$L(t) = L_\infty - (L_\infty - L_0)e^{-r_B\, t}$$

Positive solution while $L(0) = V(0) = 0$

Division by L^2 gives problems for $L \downarrow 0$

No creationism needed just mathematics

Conditions at fertilisation

Division by zero volume for the energy reserves $[E](a)$ at $a = 0$ is not possible and therefore the initial conditions are not well defined

Assume that at a small age a_0 amount of energy reserves supplied by mother to embryo equals $E(a_0) = E_0$
Regular perturbation gives

$$V(a_0) = \left(\frac{\{\dot{p}_{Am}\}}{3[E_m]} a_0 \right)^3$$

$$[E](a_0) = \frac{E_0}{V(a_0)} = E_0 \left(\frac{\{\dot{p}_{Am}\}}{3[E_m]} a_0 \right)^{-3}$$

$$E_H(a_0) = \frac{1-\kappa}{\kappa} [E_G] \left(\frac{\{\dot{p}_{Am}\}}{3[E_m]} a_0 \right)^3 \frac{\dot{k}_M}{\dot{k}_i}$$

Alternatively experimental data at a_0 can be used

Aging model

The ageing module of DEB theory is based on respiration dependent production of (self-replicating) damaging compounds
Generalisation of Gompertz and Weibull models

Two additional i-state DEB variables depending on specific growth rate $\dot{r} = \frac{dV}{da}/V$: acceleration $\ddot{q}(a)$ and hazard rate $\dot{h}_a(a)$

$$\frac{d}{da}\ddot{q} = (\ddot{q}\frac{V}{V_m}s_G + \ddot{h}_a)e(\frac{\dot{v}}{V^{1/3}} - \dot{r}) - \dot{r}\ddot{q}\ , \quad \frac{d}{dt}\dot{h}_a = \ddot{q} - \dot{r}\dot{h}_a$$

The initial conditions for a newborn read

$$\ddot{q}(0) = 0\ , \quad \dot{h}_a(0) = 0$$

s_G and $\ddot{h}_a$ are parameters

Population variable

Individual level $S(a)$ survival function describes the loss of individuals due to back-ground mortality

$$\frac{dS}{da} = -\dot{h}_a S(a) \ , \quad S(0) = 1$$

Population level $N(t)$ is used when ageing and/or other losses via interaction with environment

$$\frac{dN}{dt} = -\dot{h}_a N(t) \ , \ \text{ plus other loss rates} \ , \quad N(0) = N_0$$

We used i-state variable $H(a) = E_H(a) + E_R(a)$ the cumulative energy allocated to maturity and reproduction

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CPM Generations $i = 0 \cdots n$

Use of the Lagrangian description following Cohorts lifelong

Two individuals with the same i-state at fertilisation remain identical lifelong, that is have the same i-states for all $a \geq 0$

Periodical, Synchronous, Iteroparous reproduction

Generations $i = 0 \cdots n$, n is maximum age and also the last year of reproduction after which death

Reformulate the problem in terms of the classical nonlinear dynamical system theory by vector of state variables for whole population

$$\mathbf{X} = \Big(V_0 \cdots V_n \quad E_0 \cdots E_n \quad H_0 \cdots H_n \quad S_0 \cdots S_n \quad N_0 \cdots N_n \quad X \Big)^T$$

Growth end of year from begin of year

$$
\begin{pmatrix} \tilde{V}_0 \\ [\tilde{E}_0] \\ \tilde{H}_0 \\ \tilde{S}_0 \\ \\ \tilde{V}_i \\ [\tilde{E}_i] \\ \tilde{H}_i \\ \tilde{S}_i \\ \\ \tilde{V}_n \\ [\tilde{E}_n] \\ \tilde{H}_n \\ \tilde{S}_n \\ \\ \tilde{N}_1 \\ \\ \tilde{N}_i \\ \\ \tilde{N}_n \\ \\ \tilde{X} \end{pmatrix}
=
\begin{pmatrix} \int_0^{365} dV_0 \\ \int_0^{365} d[E_0] \\ \int_0^{365} dH_0 \\ \int_0^{365} dS_0 \\ \\ \int_0^{365} dV_i \\ \int_0^{365} d[E_i] \\ \int_0^{365} dH_i \\ \int_0^{365} dS_i \\ \\ \int_0^{365} dV_n \\ \int_0^{365} d[E_n] \\ \int_0^{365} dH_n \\ \int_0^{365} dS_n \\ \\ \int_0^{365} dN_1 \\ \\ \int_0^{365} dN_i \\ \\ \int_0^{365} dN_n \\ \\ \int_0^{365} dX \end{pmatrix}
+
\begin{pmatrix} V_0^j \\ [E_0]^j \\ H_0^j \\ S_0^j \\ \\ V_i^j \\ [E_i]^j \\ H_i^j \\ S_i^j \\ \\ V_n^j \\ [E_n]^j \\ H_n^j \\ S_n^j \\ \\ N_0^j \\ \\ N_i^j \\ \\ N_n^j \\ \\ X^j \end{pmatrix}
$$

Reproduction

begin of next year end of year

$$
\begin{pmatrix}
V_0^{j+1} \\ [E_0]^{j+1} \\ H_0^{j+1} \\ S_0^{j+1} \\ \\ V_i^{j+1} \\ [E_i]^{j+1} \\ H_i^{j+1} \\ S_i^{j+1} \\ \\ V_n^{j+1} \\ [E_n]^{j+1} \\ H_n^{j+1} \\ S_n^{j+1} \\ \\ N_0^{j+1} \\ \\ N_i^{j+1} \\ \\ N_n^{j+1} \\ \\ X^{j+1}
\end{pmatrix}
=
\begin{pmatrix}
V_0 \\ [E_0] \\ E_{H0} \\ S_0 \\ \\ \tilde{V}_{i-1} \\ [\tilde{E}_{i-1}] \\ \min(\tilde{H}_{i-1}, E_H^p) \\ \tilde{S}_{i-1} \\ \\ \tilde{V}_{n-1} \\ [\tilde{E}_{n-1}] \\ \min(\tilde{H}_{n-1}, E_H^p) \\ \tilde{S}_{n-1} \\ \\ \sum_{k=1}^{n} \kappa_R \max(\tilde{H}_k - E_H^p, 0)\tilde{N}_k / E_0 \\ \\ \tilde{N}_{i-1} \\ \\ \tilde{N}_{n-1} \\ \\ \tilde{X}
\end{pmatrix}
$$

Assumption that environment is periodically (one year) where the time of reproduction is used as the monitoring date ($a = 0$)

The time is indicated by
super-index $j = mod(t, 365)$ in days

sub-index i counts the generations starting at the beginning of the time intervals $j \cdots j + n$

age of an individual $= 365i + a$ and lives at time $t = 365(j + i) + a$

Hence, state variables are only piecewise smooth with cyclic boundary conditions and jumps (from emptying reproduction buffer) and boundary condition at age $a = 0$ of the first year cohort

Stroboscopic map

In the first step for with-in year dynamics solving the set of couple ode equations for DEB variables together

In the second step reproduction rules (emptying reproduction differ and formation of embryo's form the model)

A stroboscopic (next-generation) map Φ is defined as

$$\mathbf{X}^{j+1} = \Phi\left(\mathbf{X}^{j}\right),$$

where $j \cdots$ denotes an iteration of generations

Analysis

Calculation of the fixed points of map gives equilibrium of the age distributions for the i-states and the p-state

Equilibrium or fixed point conditions:

$$\mathbf{X}^{j+1} = \mathbf{X}^{j}$$

$$V_i^{j+1} = V_i^{j}\ , \quad [E_i]^{j+1} = [E_i]^{j}\ , \quad E_{Hi}^{j+1} = E_{Hi}^{j}\ , \quad S_i^{j+1} = S_i^{j}$$
$$N_i^{j+1} = N_i^{j}\ , \quad X^{j+1} = X^{j}\ , \quad i = 0, \cdots n\ , \quad j \leq 0$$

Numerical solution obtained by a combination of an ODE-solver and Newtonian method to solve the nonlinear set of equations, similar to calculation of limit cycle

Food–population model

Constant food:

Scaled Holling type II functional response $f(X)$ with X_k is half-saturation constant

Population is studied in a semi-chemostat environment where food concentration $X(t)$ and food concentration inflow with X_{in} time-dependent

$$\frac{dX}{dt} = D(X_{in}(t) - X(t)) - \{\dot{p}_{Xm}\} f(X(t)) \sum_{i=0}^{n} (V_i^{2/3} N_i)$$

where embryos do not feed

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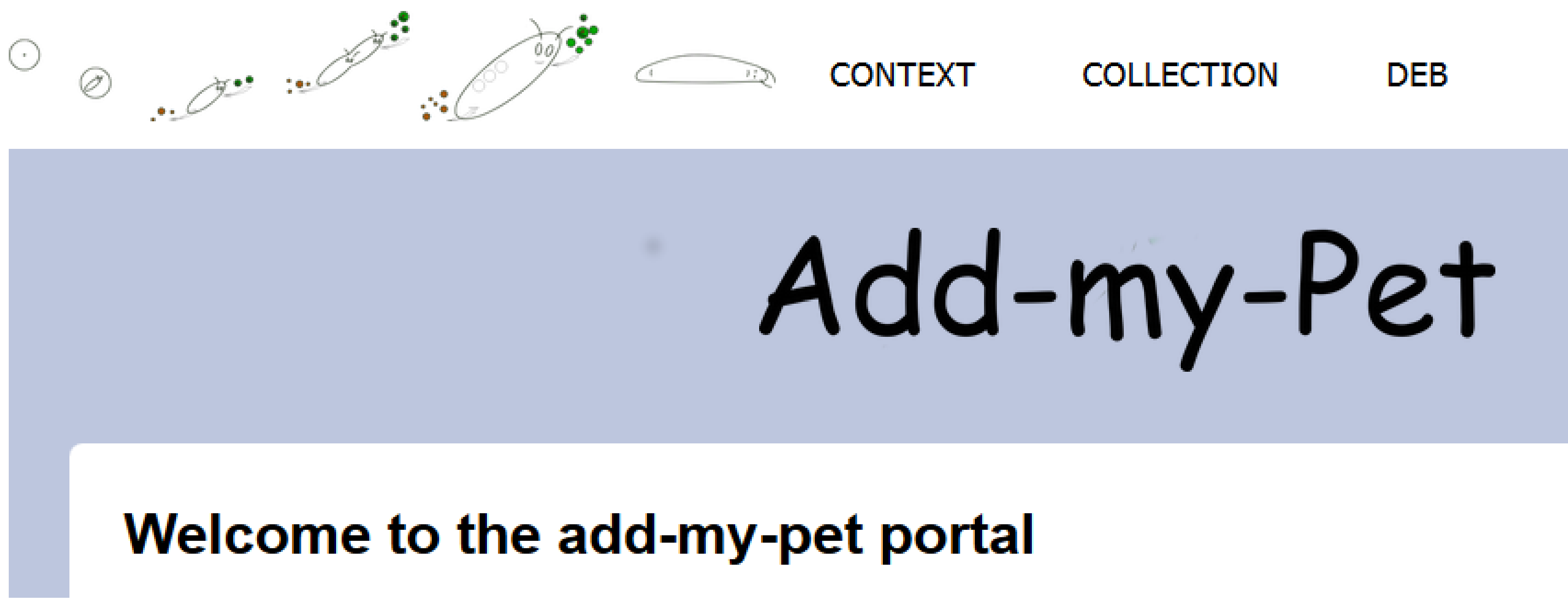
Add-my-Pet collection

https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/index.html



Add-my-Pet collection

Application: Population dynamics

https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/index.html

Files with code and parameter values

Marbled electric ray *Torpedo marmorata*

https://en.wikipedia.org/wiki/Torpedo_morata

From AmP-tool package results to population dynamics

- Individual: AmP-tool package results

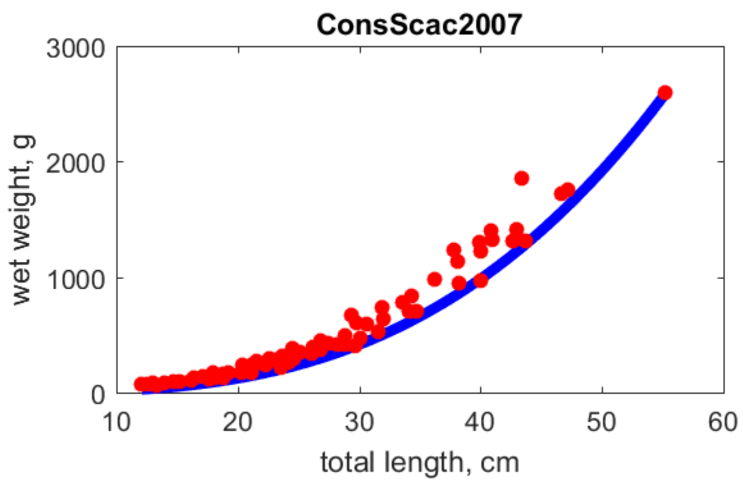
- Individual: Lifelong development of one individual

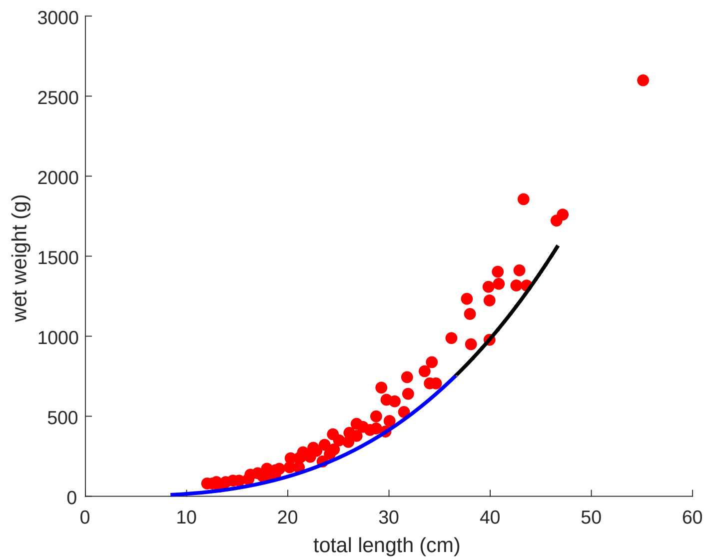
- Individual–Population: Lifelong development of one individual split-up in generations

- Population: Development of all n generations

AmP-tool package results

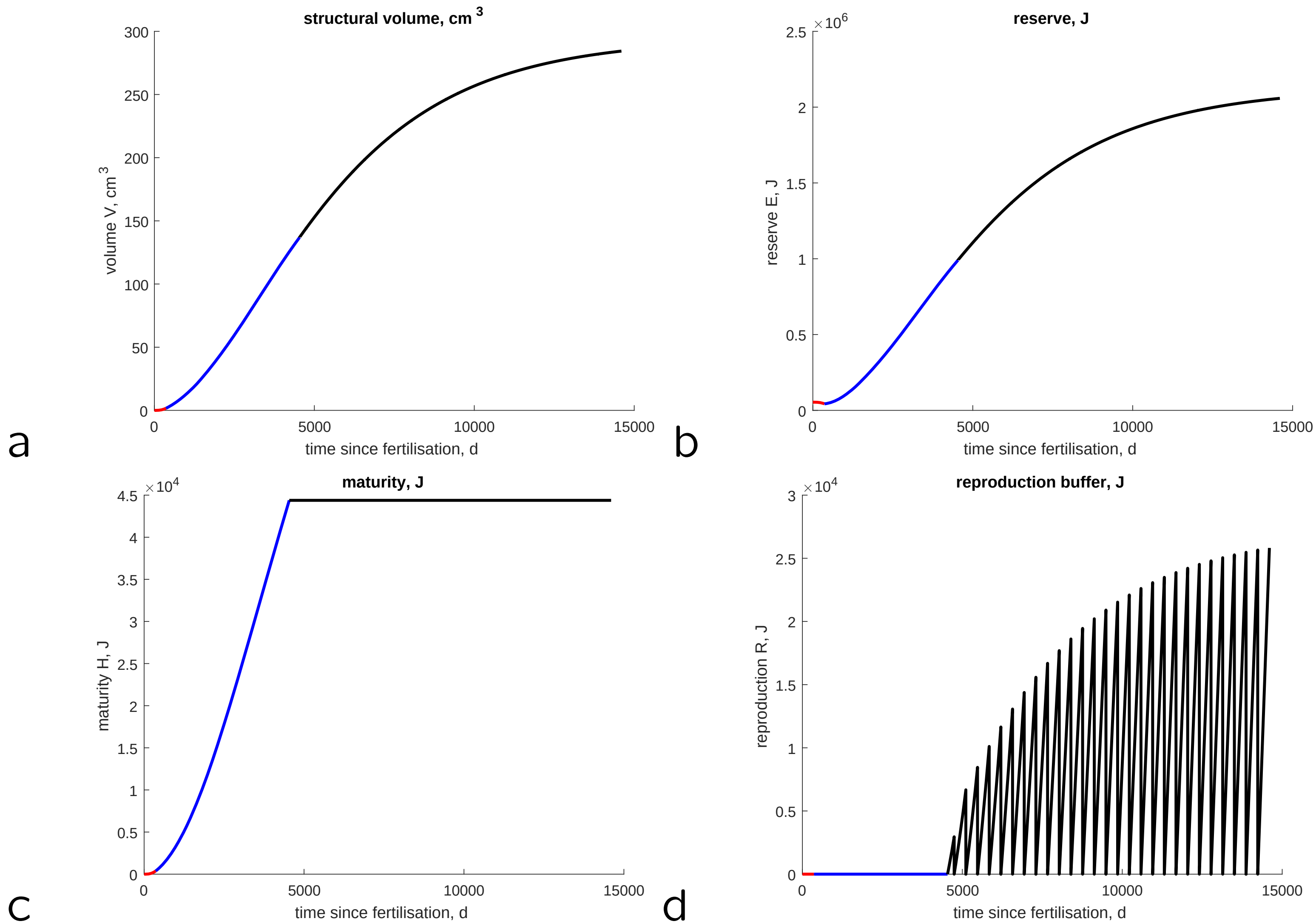
Calculated total wet-weight species $W_w(a)$ and experimental data





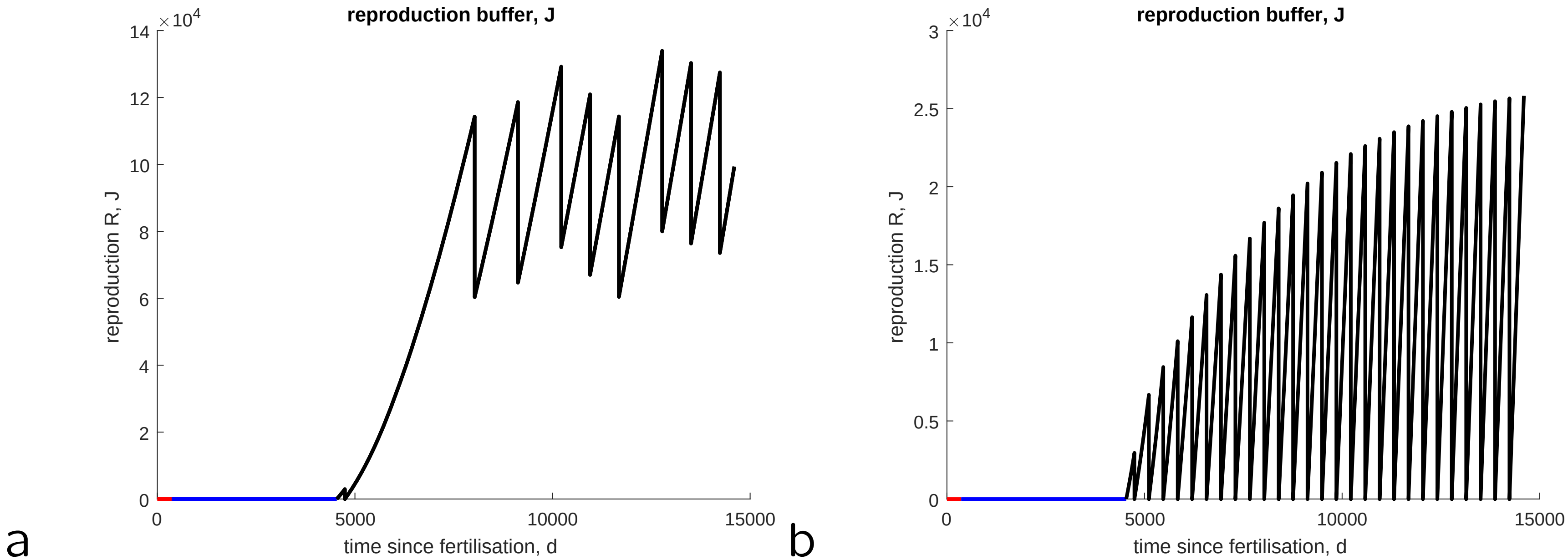
Left: result from AmP-tool package. Right: results from total life cycle calculations.

Data from: Consalvo, I., Scacco, U., Romanelli, M., and Vacchi, M. (2007). Comparative study on the reproductive biology of *Torpedo torpedo* (Linnaeus, 1758) and *T. marmorata* (Risso, 1810) in the central Mediterranean Sea. SCIENTIA MARINA, Barcelona (Spain), 71.



a: $V(a)$ [cm^3], b: $E(a)$ [J], c: $E_H(a)$ [J], d: $E_R(a)$ [J], embryo juv adult

Energy in reproduction buffer $E_R(a)$ [J]



a: discrete reproduction and b: continuous reproduction

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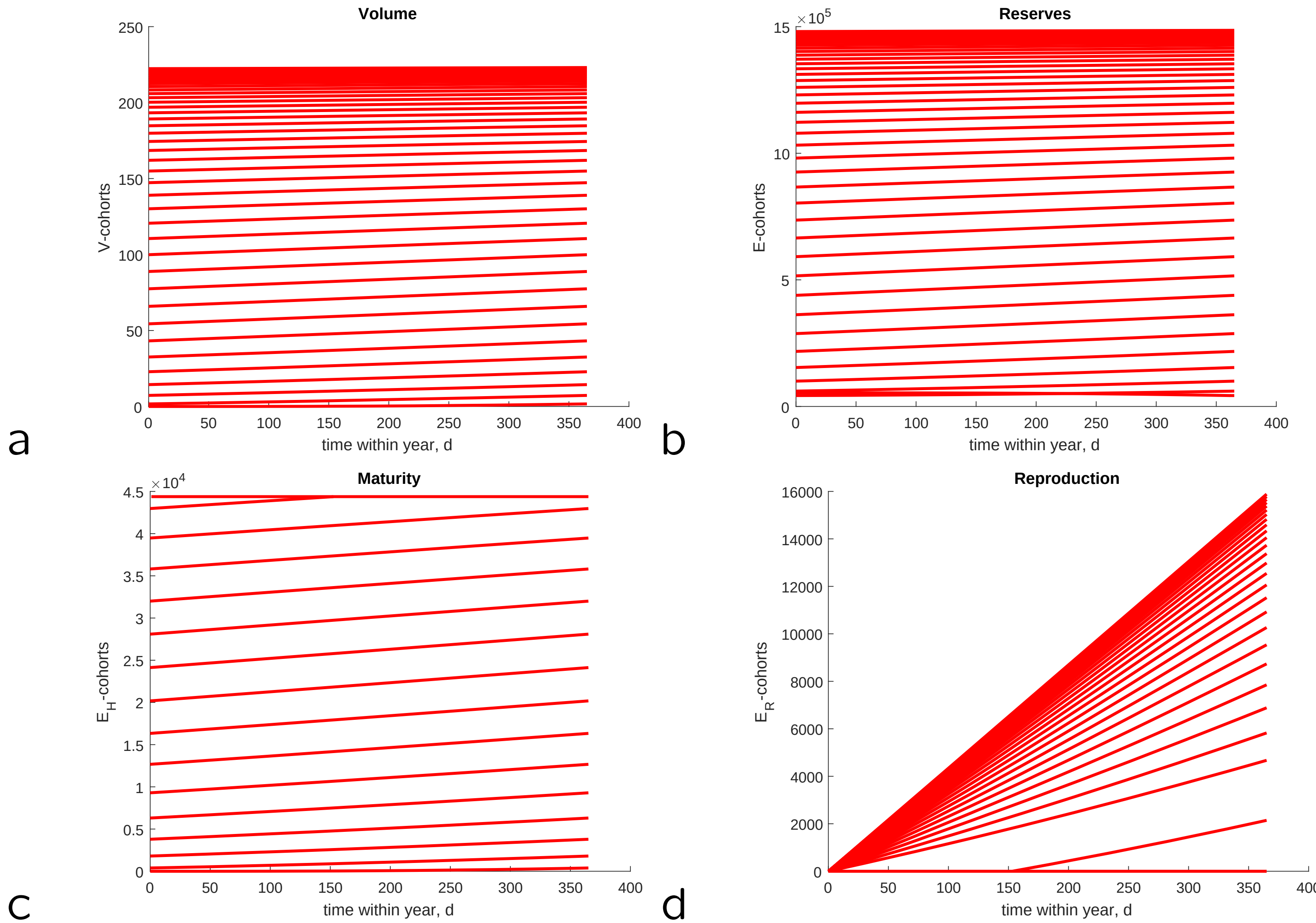
Calculation of f such that there is an equilibrium

This equilibrium is neutral stable



a: $V(a)$ [cm^3], b: $E(a)$ [J], c: $E_H(a)$ [J], d: $E_R(a)$ [J]

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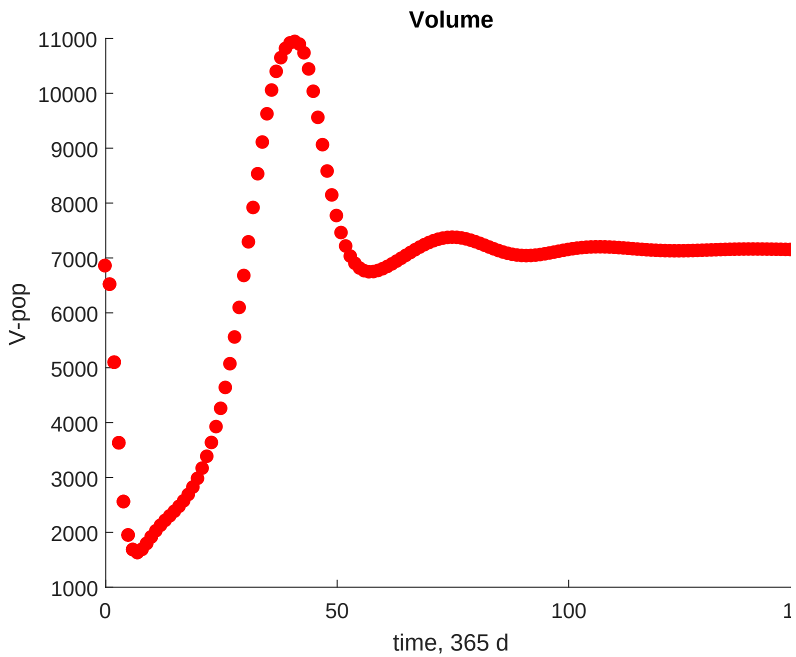
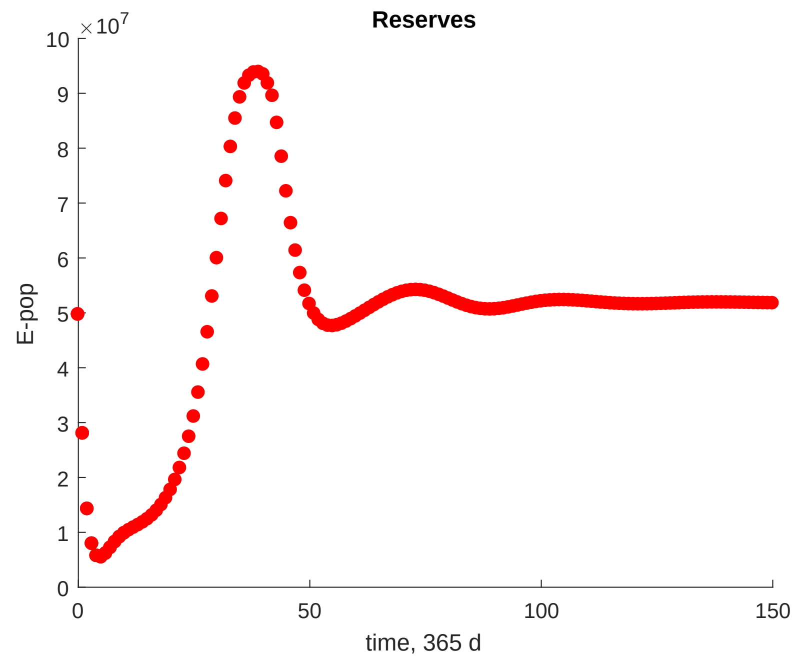
$$\frac{dX}{dt} = D(X_{in}(t) - X(t)) - \{\dot{p}_{Xm}\} f(X(t)) \sum_{i=0}^{n} V_i^{2/3} N_i$$

Food–population model $j = 0 \cdots 150$

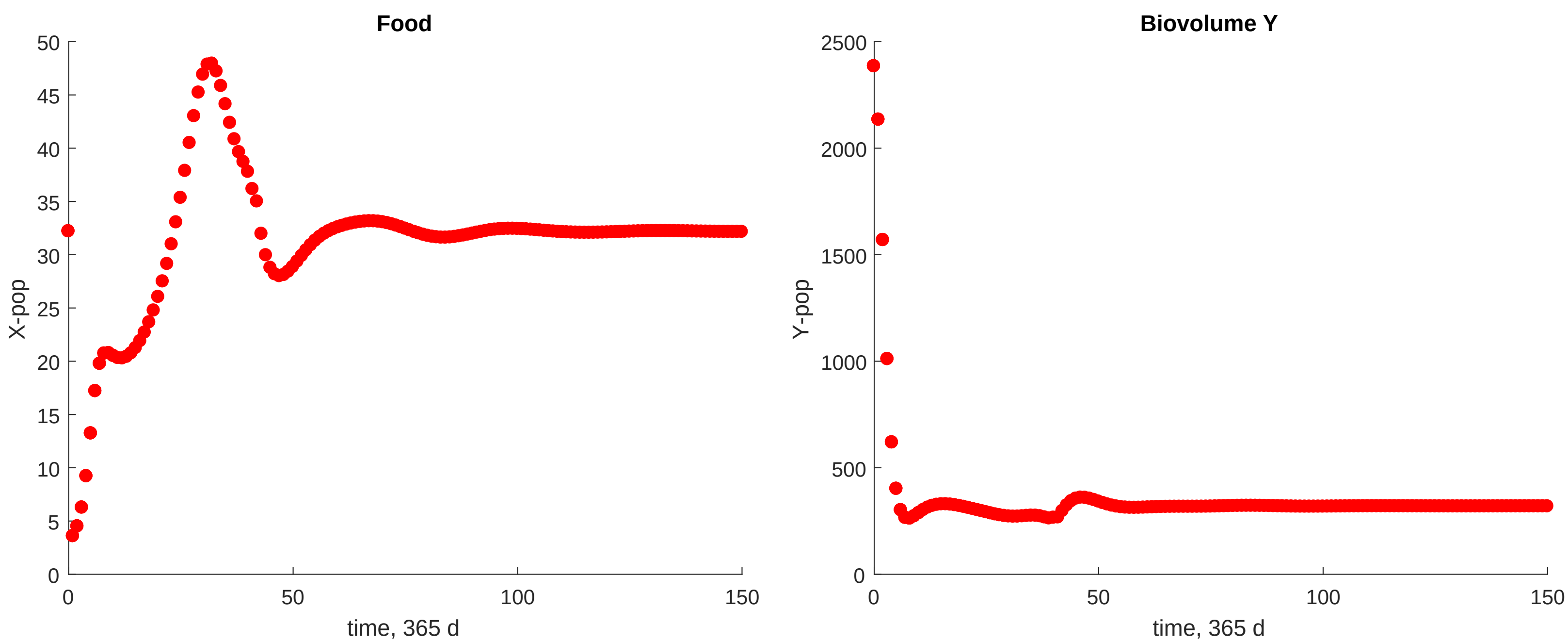




Volume: $V^j = \sum_{k=0}^{n} V_k^j$

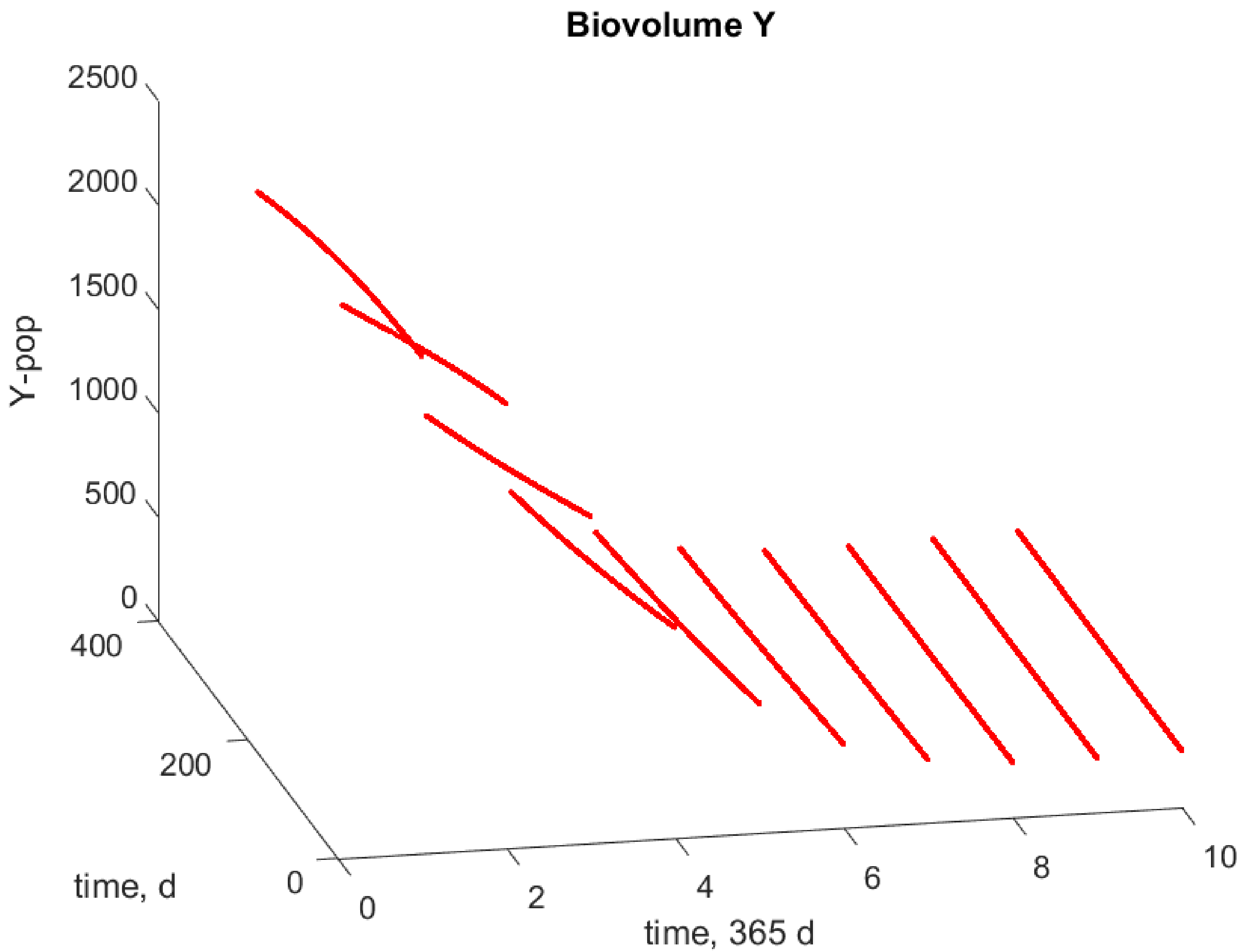
Reserve: $E^j = \sum_{k=0}^{n} E_k^j$

Population p-state variables: $j = 0 \cdots 150$



Food X^j

Biovolume $Y^j = \sum_{k=0}^{n} V_k^j N_k^j$



Population structural biovolume: $Y(a) = \sum_{k=0}^{n} V_k(a) N_k(a)$

Conclusions

- Interface for building population model using individual DEB model with estimated parameter values

- First single age-dependent life-cycle where empirical data were used to lifelong interval

- Show of use of time-dependent model in simple semi-chemostat population–food in chemostat

Conclusions

- Lagrange description: following cohort of identical DEB individuals
- Population consists of finite generations, number equal to maximum age
- Population state is defined as the number of individuals within each generation just after fertilisation whereby the with-in year development can be derived

- Derived finite dimensional map can be analysed in the similar way as the Leslie-matrix type discrete matrix models

- Coupling with other structured population model analysis approaches: *e.g.* Escalator Boxcar Train, I(A)BM, IPM method, PDE, renewal equation

- Post-processing with code for calculation of individual dynamics freely downloadable software AmP-tool

Literature

Anonymous. (2019). *Add-my-Pet* https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/.

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