A canonical ecosystem model

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Abstract

The canonical community (or ecosystem) model consists of a coupled set of non-linear differential equations, that describe the rate of change of the size of producer, consumer and decomposer populations, various types of detritus, and the nutrients carbon dioxide and ammonium.

All populations are described by a V1-morph DEB model, with either one or two reserve compartments. The system is closed for matter.

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Paper

Conservation Physiology

Volume 10 • 2022 10.1093/conphys/coac057

SEB SOCIETY FOR EXPERIMENTAL BIOLOGY

Research article

A simple DEB-based ecosystem model

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Figure 1: Embroidering on earlier work by Bas Kooijman and Roger Nisbet, this paper describes in detail a canonical community model based on DEB theory.

Content

- The future of global marine food systems
- DEB V1-morphs
- Synthesizing Units: Holling, parallel processing, and preference
- The canonical model
- Parametrization
- Model dynamics

The future of global marine food systems

- How much food can the oceans and seas provide, after a fisheries-aquaculture transition?
- An ecosystem-based view with an emphasis on energy fluxes and nutrient and mass balances in marine systems
- Use DEB theory

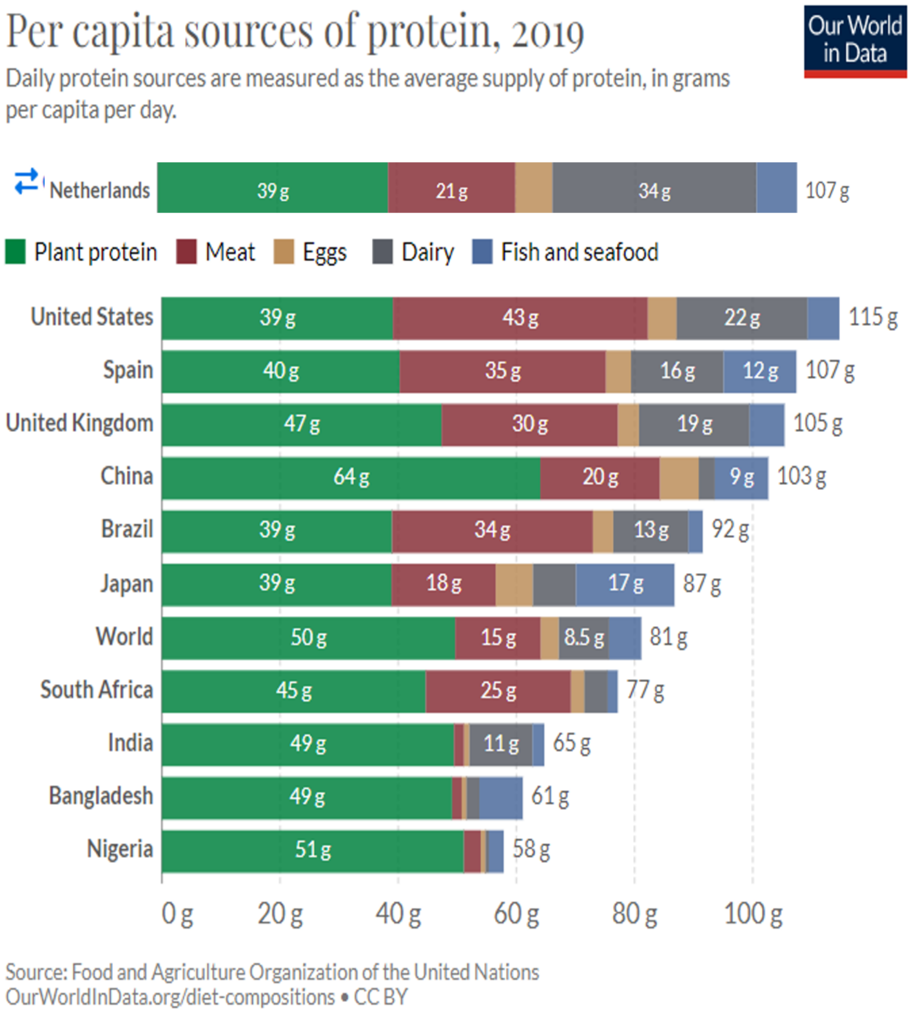

Figure 2: Protein intake.

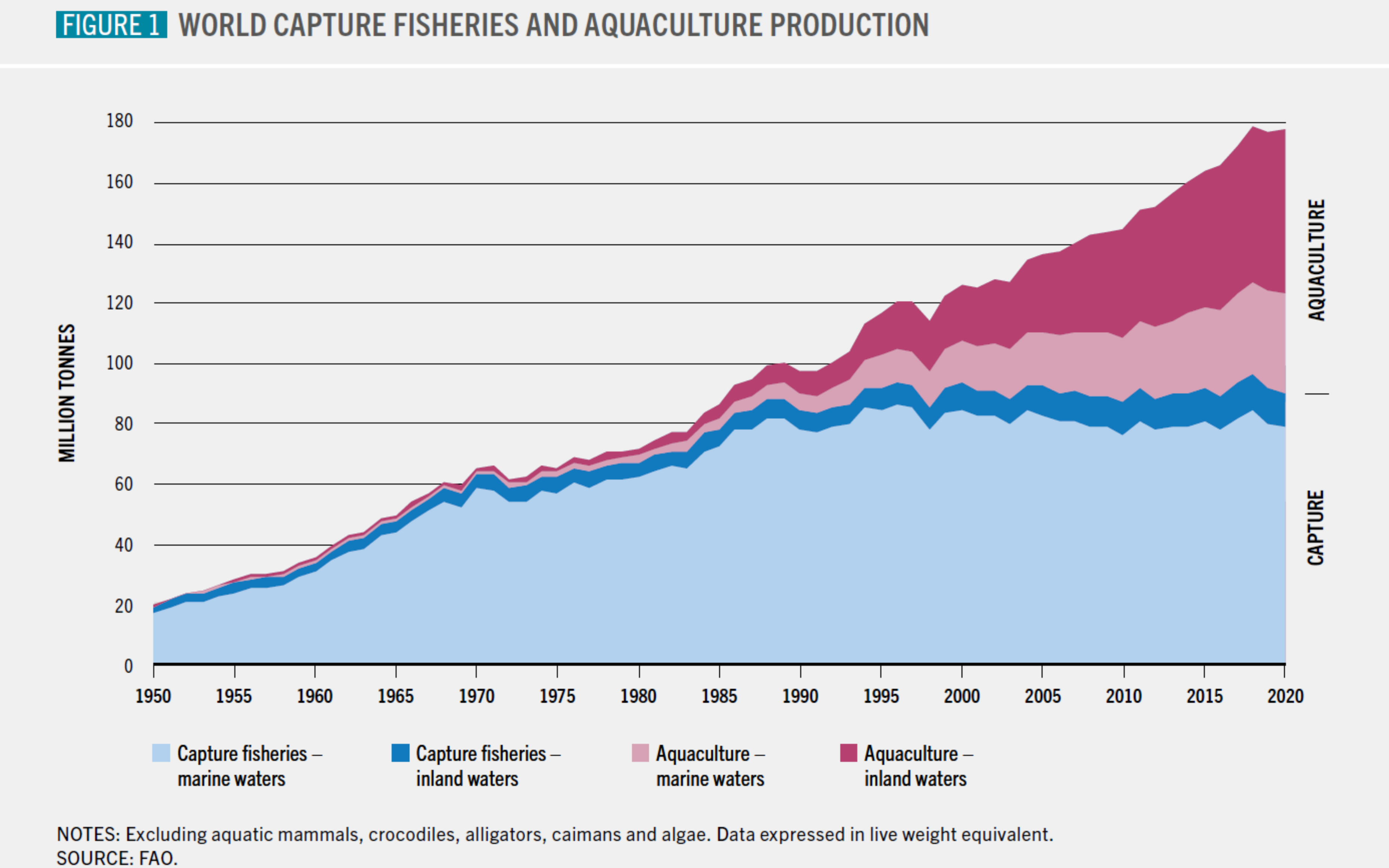

Figure 3: Fishery and aquaculture yields.

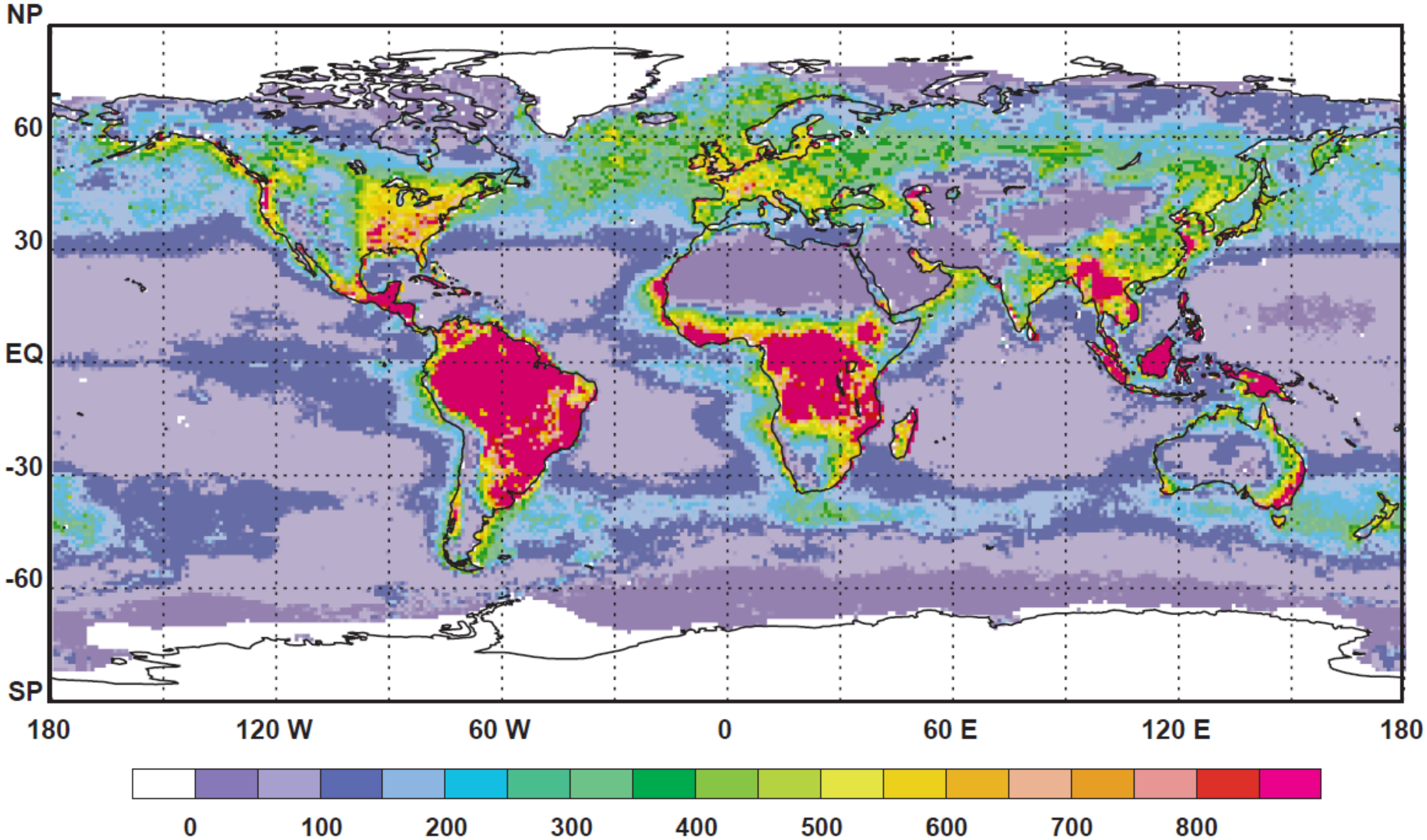

Figure 4: Global primary production.

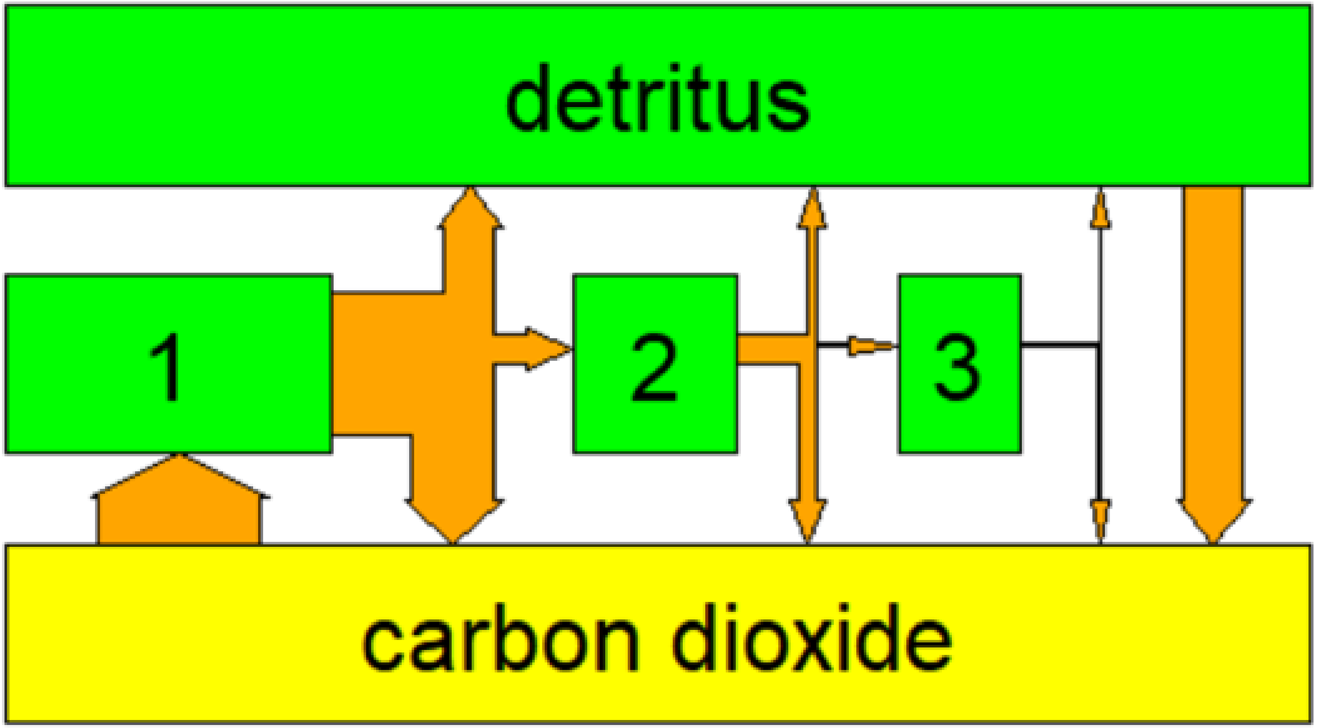

Figure 5: The cycle of life.

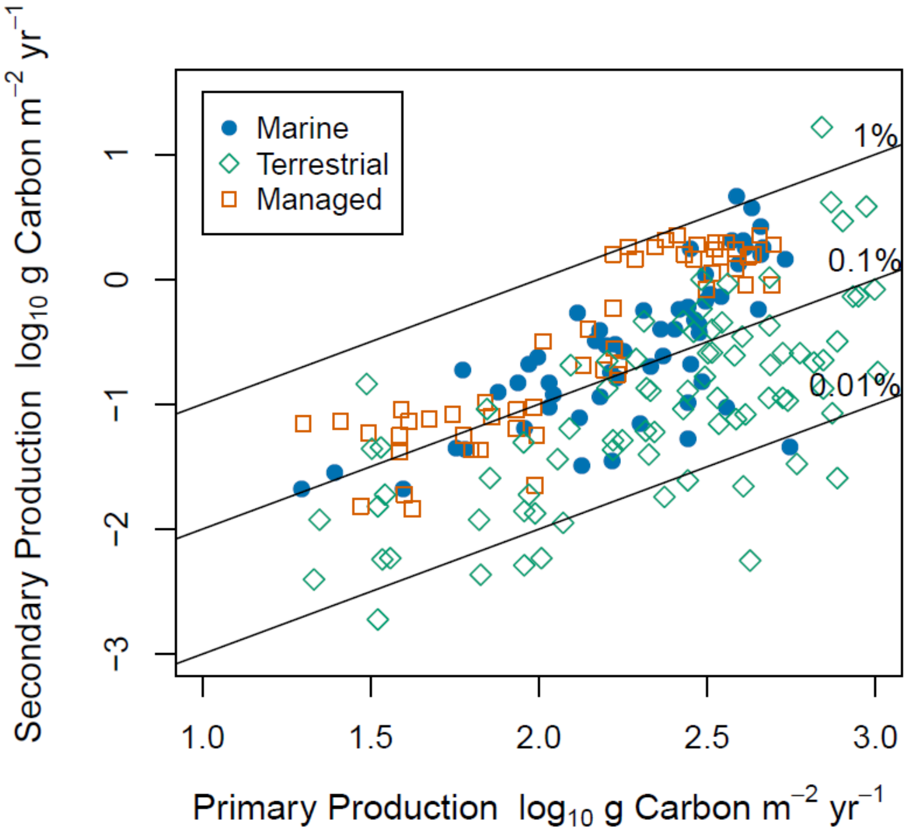

Figure 6: Secondary production or fisheries yield versus primary productivity.

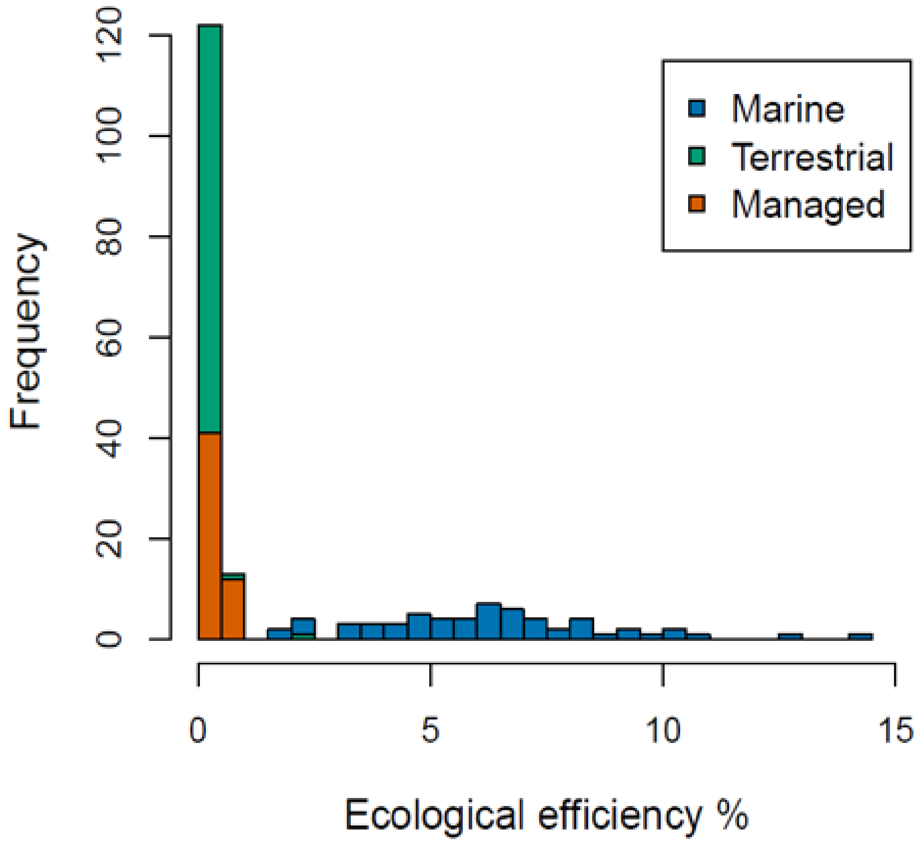

Figure 7: Trophic efficiency.

Lessons from farming and ecology

- Finfish aquaculture at sea is not a very promising avenue to increase ‘true’ marine food production
- Replace hardly harvestable phytoplankton and zooplankton by seaweed and shellfish
- Take account of possible nutrient depletion and decreasing primary production
- Consider effects on natural values and biodiversity

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Figure 8: Further reading.

Received: 3 March 2023 | Revised: 24 April 2023 | Accepted: 25 April 2023

DOI: 10.1002/fes3.464

Food and Energy Security WILEY

ORIGINAL ARTICLE

The carrying capacity of the seas and oceans for future sustainable food production: Current scientific knowledge gaps

Jaap van der Meer[1,2] | Myriam Callier[3] | Gianna Fabi[4] | Luc van Hoof[1] | J. Rasmus Nielsen[5] | Saša Raicevich[6]

Figure 9: Further reading.

V1-morphs

Assimilation rate $\dot{p}_A$ is proportional to surface area, which is proportional to volume V for V1-morphs. Hence

$$\dot{p}_A = f[\dot{p}_{Am}]V \tag{1}$$

where f is the scaled functional response and $[\dot{p}_{Am}]$ is the volume-specific assimilation rate.

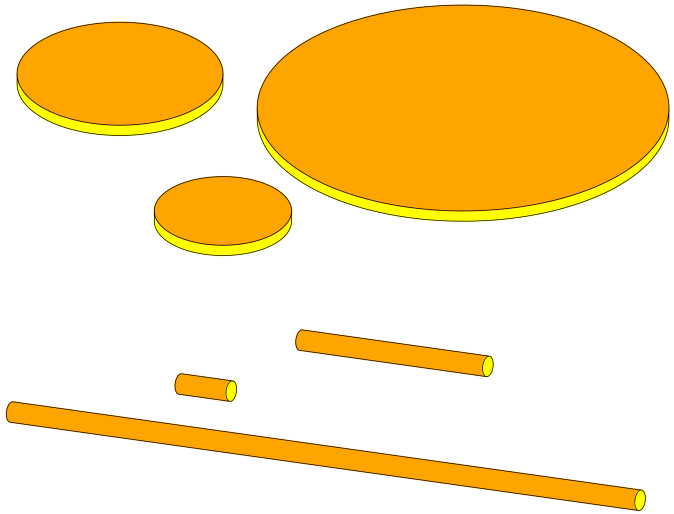

Figure 10: A rope growing in length and a pancake growing in diameter are both V1-morphs. The area responsible for the uptake of resources is coloured orange.

Reserve density follows first order dynamics

$$\frac{\mathrm{d}[E]}{\mathrm{d}t} = \frac{\dot{p}_A}{V} - \dot{k}_E[E] = f[\dot{p}_{Am}] - \dot{k}_E[E] \tag{2}$$

and the differential does not depend upon volume, but only upon reserve density. The parameter $\dot{k}_E$ has been given the name specific energy conductance. It has the physical dimension per time.

Reserve dynamics is given by the assimilation rate minus the mobilization rate

$$\frac{\mathrm{d}[E]V}{\mathrm{d}t} = V\frac{\mathrm{d}[E]}{\mathrm{d}t} + [E]\frac{\mathrm{d}V}{\mathrm{d}t} = \dot{p}_A - \dot{p}_C \tag{3}$$

Thus,

$$V\left(\frac{\dot{p}_A}{V}-\dot{k}_E[E]\right)+[E]\frac{\mathrm{d}V}{\mathrm{d}t}=\dot{p}_A-\dot{p}_C \tag{4}$$

and the mobilization rate thus equals

$$\dot{p}_C=\dot{k}_E[E]V-[E]\frac{\mathrm{d}V}{\mathrm{d}t} \tag{5}$$

where the latter term prevents dilution by growth.

For organisms that simply divide into two daughter cells, and which are classified as juveniles in DEB terminology, κ can be set equal to one. Hence the allocation is given by

$$\dot{p}_C = [E_G]\frac{\mathrm{d}V}{\mathrm{d}t} + [\dot{p}_M]V \tag{6}$$

Substituting equation 5 in equation 6 gives the growth equation

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \frac{\dot{k}_E[E] - [\dot{p}_M]}{[E] + [E_G]}V \tag{7}$$

Under constant food conditions, the reserve density is in equilibrium

$$\frac{\mathrm{d}[E]}{\mathrm{d}t} = f[\dot{p}_{Am}] - \dot{k}_E[E] = 0 \tag{8}$$

and proportional to the scaled functional response

$$[E]^* = \frac{f[\dot{p}_{Am}]}{\dot{k}_E} \tag{9}$$

The growth equation simplifies to

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \frac{[\dot{p}_{Am}]f - [\dot{p}_M]}{[\dot{p}_{Am}]f\dot{k}_E^{-1} + [E_G]}V = \dot{r}V \tag{10}$$

where $\dot{r}$ is the specific growth rate. Hence, the growth rate of the structural volume is proportional to the structural volume itself. V1-morphs show exponential growth at constant food density.

A mass-mass framework

DEB models are usually written in an energy-volume framework, but one might choose to write the reserve dynamics and the growth equation in a mass-mass framework.

Structural body mass M_V is given by $[M_V]V$, where $[M_V]$ is the specific density of the structural body expressed in C-moles per volume. Reserve mass M_E is given by E/μ_E, where μ_E is the potential energy of the reserves expressed in energy per C-mole.

Hence, reserve density m_E in terms of reserve mass per unit of structural mass is given by

$$m_E = \frac{M_E}{M_V} = \frac{E}{\mu_E[M_V]V} = \frac{[E]}{\mu_E[M_V]} \tag{11}$$

EXERCISE

Re-write equations 2 and 7 in a mass-mass framework

$$\frac{\mathrm{d}[E]}{\mathrm{d}t} = f[\dot{p}_{Am}] - \dot{k}_E[E]$$

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \frac{\dot{k}_E[E] - [\dot{p}_M]}{[E] + [E_G]}V$$

using $M_V = [M_V]V$ and $m_E = [E]/(\mu_E[M_V])$

Equation 2 becomes

$$\frac{\mathrm{d}m_E}{\mathrm{d}t} = \frac{\mathrm{d}[E]}{\mathrm{d}t}\frac{1}{\mu_E[M_V]} = \frac{f[\dot{p}_{Am}] - \dot{k}_E[E]}{\mu_E[M_V]} = f j_{EAm} - \dot{k}_E m_E \tag{12}$$

and Equation 7 becomes

$$\frac{\mathrm{d}M_V}{\mathrm{d}t} = \frac{\mathrm{d}V}{\mathrm{d}t}[M_V] = \frac{\dot{k}_E[E] - [\dot{p}_M]}{[E] + [E_G]}[M_V]V = \frac{\dot{k}_E m_E - j_{EM}}{m_E + y_{EV}} M_V \tag{13}$$

Table 1: Primary parameters of the DEB model for V1-morphs, specific for a mass-mass framework. The last column indicates the relationship with the parameters from the energy-length framework that has been replaced.

Symbol	Dimension	Interpretation	Relationship
j_{EAm}	$\#\#^{-1}t^{-1}$	Mass-specific maximum assimilation rate	$[\dot{p}_{Am}] = \mu_E[M_V]j_{EAm}$
j_{EM}	$\#\#^{-1}t^{-1}$	Mass-specific maintenance rate	$[\dot{p}_M] = \mu_E[M_V]j_{EM}$
y_{EV}	$\#\#^{-1}$	Mass-specific costs of growth	$[E_G] = \mu_E[M_V]y_{EV}$

The synthesising unit and Holling's disc equation

The synthesising unit underlying Holling's disc equation serves customers (food items) one at a time and each service takes some length of time and ends with the deliverance of a product (an ingestible piece of food). Customers that find the server busy at arrival depart.

Both the interarrival time and the service time are exponentially distributed.

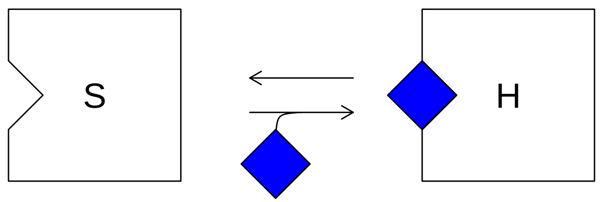

Figure 11: When a customer arrives at an empty server (S) the server becomes busy (H). Each service takes some length of time, after which the server becomes empty again.

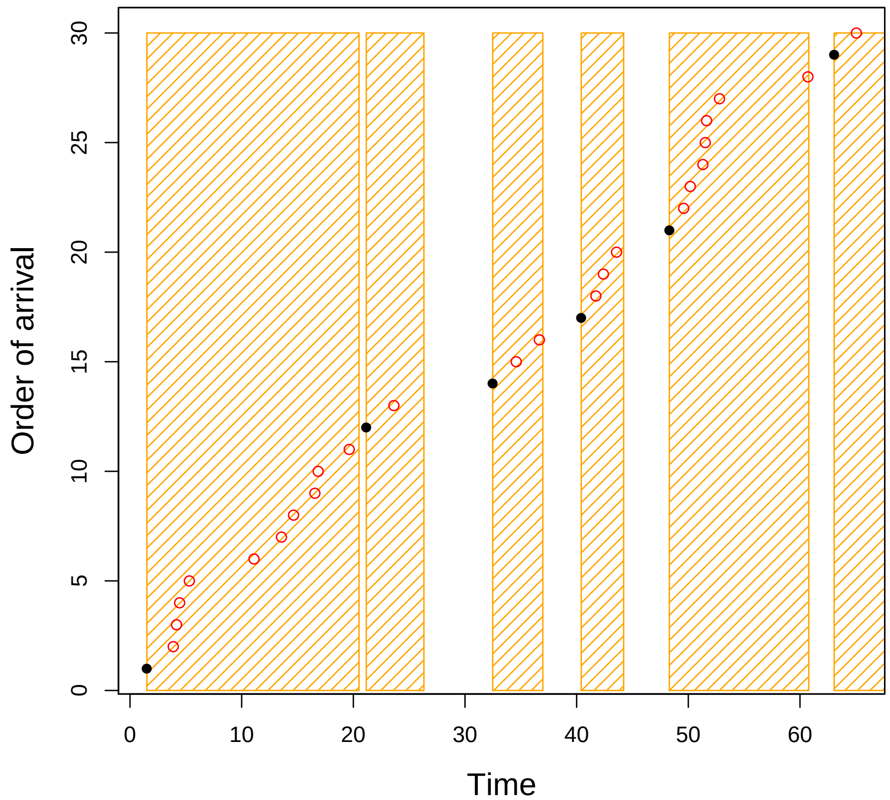

Figure 12: Customers arriving at an empty server (filled dots) are served one at a time. Each service takes some length of time (indicated by the shades areas) and ends with the deliverance of a product, at which the server becomes empty again. Arriving customers finding a busy server (open dots) depart.

The rate of change in the density of empty (S_0) and busy (S_1) servers is given by

$$\frac{\mathrm{d}S_0}{\mathrm{d}t} = -\frac{\mathrm{d}S_1}{\mathrm{d}t} = -\dot{b}XS_0 + \dot{k}S_1$$

where X is the density of customers that want to be served and $\dot{b}$ (searching rate) and $\dot{k}$ (servicing rate) are constants.

The processing rate per server, which equals $\dot{k}$ times the fraction of busy servers at equilibrium (this fraction is equivalent to the fraction of time a specific server is busy), is

$$\dot{J} = \dot{k}\frac{S_1^*}{S_0^* + S_1^*} = \dot{k}\frac{\frac{\dot{b}}{\dot{k}}XS_0^*}{S_0^* + \frac{\dot{b}}{\dot{k}}XS_0^*} = \frac{\dot{b}X}{1 + \frac{\dot{b}}{\dot{k}}X} = \dot{J}_m\frac{X}{X_K + X} \qquad (14)$$

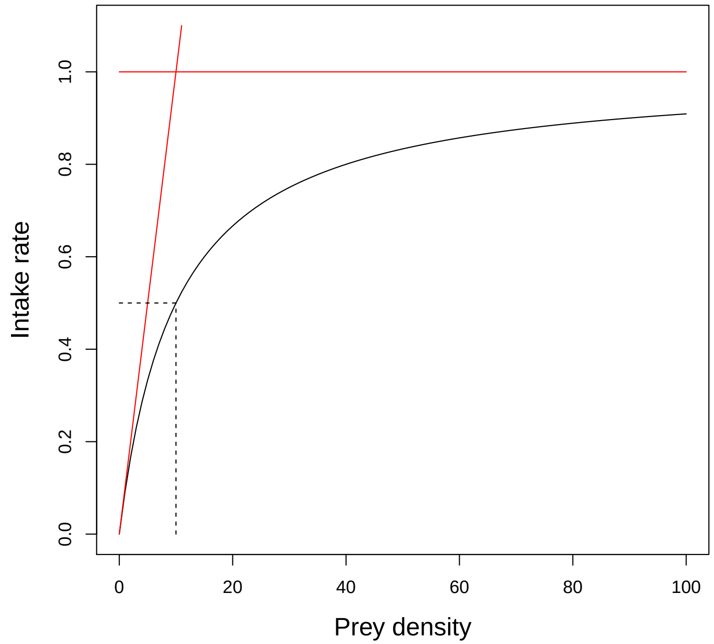

Figure 13: Holling's type II functional response equation, in which the maximum is given by the 'servicing' rate. The tangent at the origin equals the 'searching' rate. The half-saturation constant, which equals the ratio of the servicing rate and the searching rate.

Parallel processing

Consider a synthesising unit that requires two molecules, one of substrate type A and one of substrate type B, to produce a product molecule C.

Suppose further that the binding of one type of molecule does not interfere with that of the other, which may be called parallel processing.

The density of empty units is given by S_{00}, the density of those with only A bound by S_{10}, with only B by S_{01} and if both A en B are bound by S_{11}.

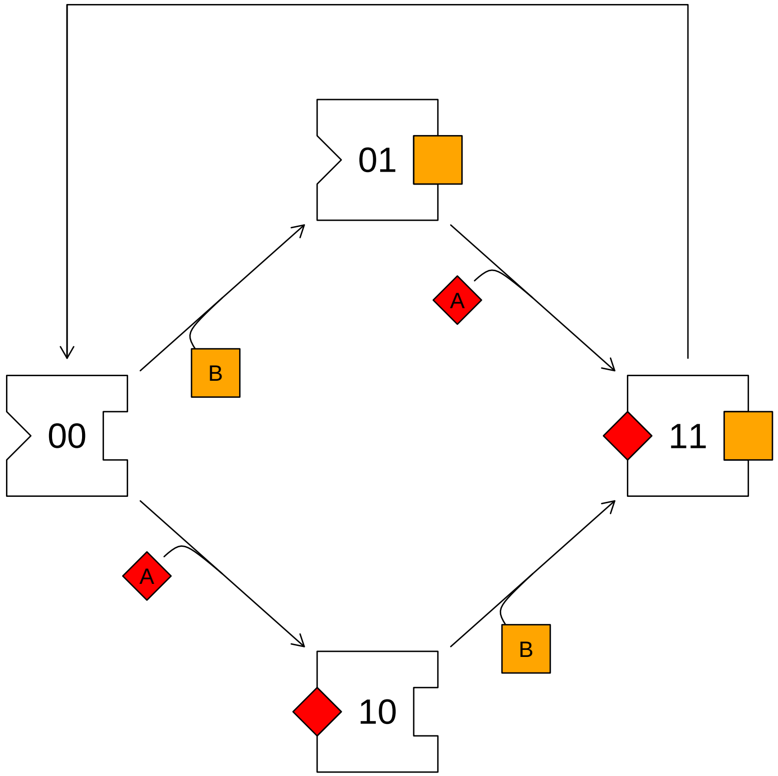

Figure 14: In parallel processing, a synthesising unit that requires two molecules, one of substrate type A and one of substrate type B, binds these two molecules in a random order. When both molecules are bound, the busy unit will produce a product molecule C after some length of time and then returns to the empty state.

The following differential equations apply:

$$
\begin{aligned}
\frac{\mathrm{d}S_{00}}{\mathrm{d}t} &= -\left(\dot{b}_A X_A + \dot{b}_B X_B\right) S_{00} + \dot{k} S_{11} \\
\frac{\mathrm{d}S_{10}}{\mathrm{d}t} &= \dot{b}_A X_A S_{00} - \dot{b}_B X_B S_{10} \\
\frac{\mathrm{d}S_{01}}{\mathrm{d}t} &= \dot{b}_B X_B S_{00} - \dot{b}_A X_A S_{01} \\
\frac{\mathrm{d}S_{11}}{\mathrm{d}t} &= \dot{b}_B X_B S_{10} + \dot{b}_A X_A S_{01} - \dot{k} S_{11}
\end{aligned}
$$

EXERCISE

Write the production rate of product C, which equals $\dot{k}$ times the fraction of busy servers

$$\dot{J}_C = \dot{k}\frac{S_{11}^*}{\sum\sum S_{ij}^*}$$

in terms of the molecule arrival rates $\dot{J}_A = \dot{b}_A X_A$ and $\dot{J}_B = \dot{b}_B X_B$

Express all equilibrium states relative to S_{11}^{*}, e.g.

$$S_{00} = \frac{\dot{k}}{\dot{J}_A + \dot{J}_B} S_{11}$$

The process rate per server (equivalent to the production rate of product C) can be written as

$$\dot{J}_C = \frac{1}{\dot{J}_{Cm}^{-1} + \dot{J}_A^{-1} + \dot{J}_B^{-1} - \left(\dot{J}_A + \dot{J}_B\right)^{-1}}$$

where $\dot{J}_{Cm} = \dot{k}$ is the maximum process rate. Thus, $\dot{J}_{Cm}^{-1}$ is the expected 'servicing' time, and $\dot{J}_A^{-1}$ and $\dot{J}_B^{-1}$ are the expected interarrival times of molecules of type A and B, respectively.

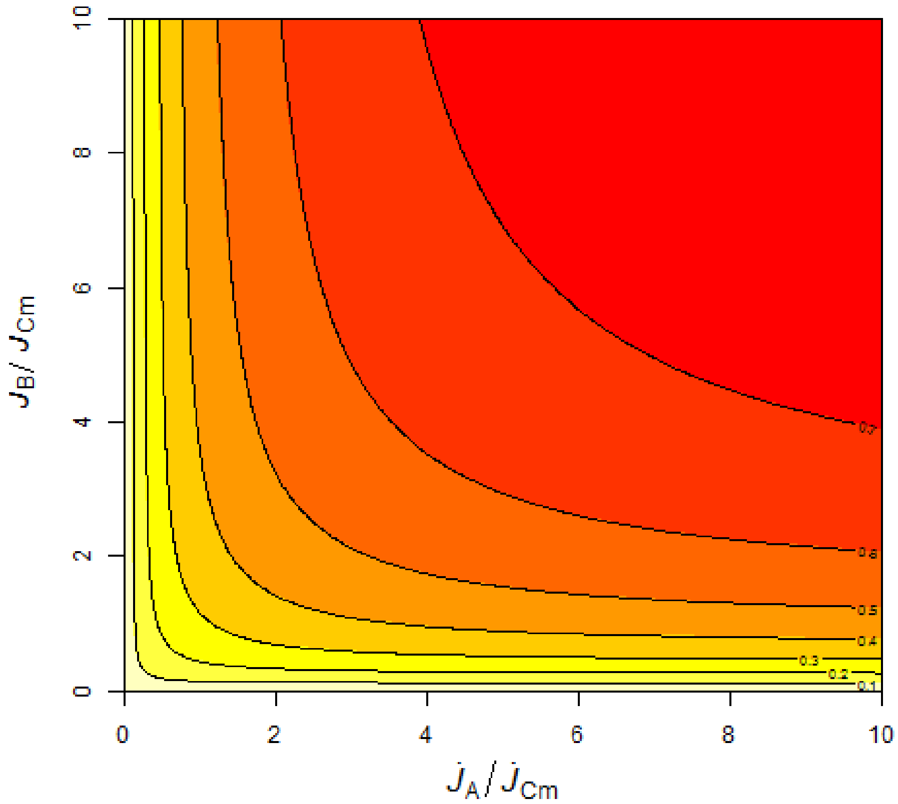

Figure 15: Contours of the production rate as a function of the rates at which molecules of substrate A and B, respectively, arrive, for a parallel processing SU that requires two molecules, one of substrate type A and one of substrate type B, to produce a molecule C.

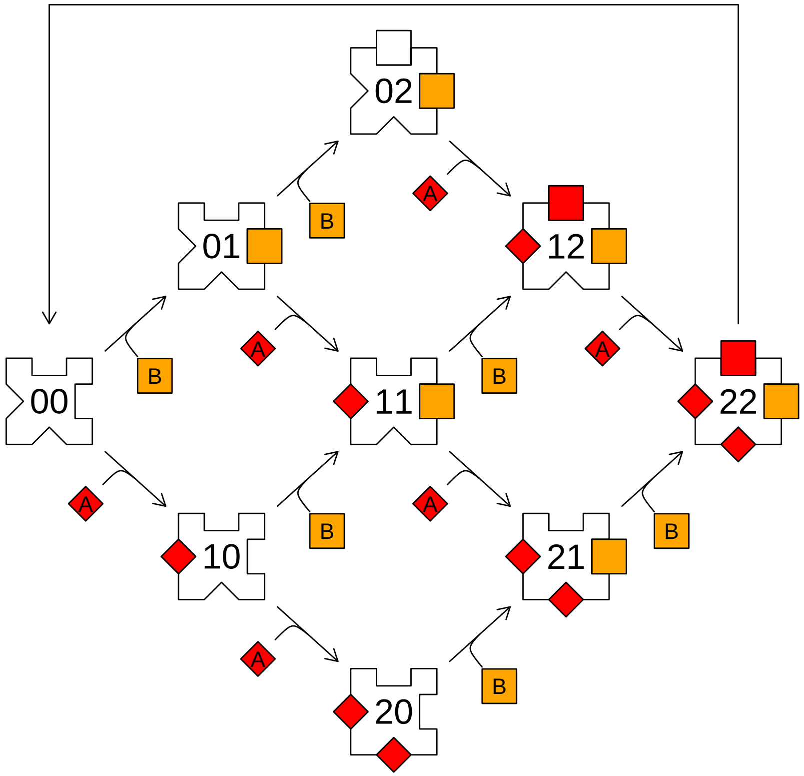

Figure 16: A parallel processing SU requiring two molecules of type A and two of type B.

Preference SU

Consider a synthesizing unit that can use two types of substrates, but has a preference for one type.

The unit is either empty (state S_0), contains the preferred substrate (S_1), or the less appreciated substrate (S_2).

If the unit is empty it will always accept a substrate once it arrives. If the unit already contains the less appreciated substrate 2 and a preferred substrate 1 arrives, it will delete type 2 and replace it by the preferred type 1.

Processing of each substrate results in the formation of product.

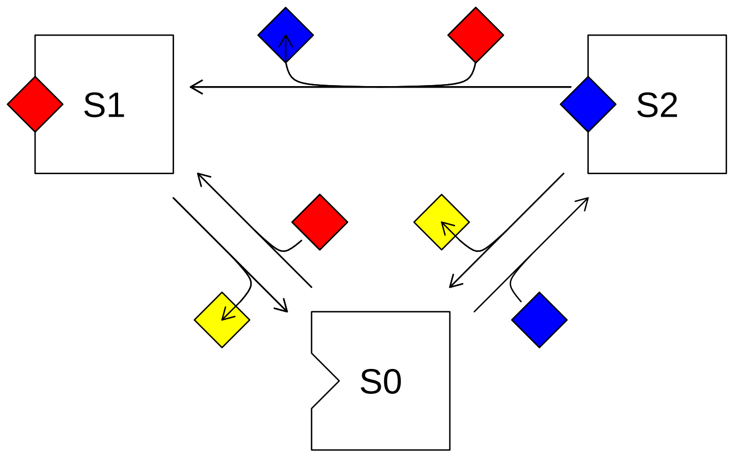

Figure 17: A preference SU accepting two types of molecules, but with a preference for one.

EXERCISE

Formulate the differential equations for this system, and (bonus question) the production rate in terms of the molecule arrival rates $\dot{J}_i = \dot{b}_i X_i$.

The following differential equations apply

$$\begin{aligned}
\frac{dS_0}{dt} &= -\left(\dot{b}_1 X_1 + \dot{b}_2 X_2\right) S_0 + \dot{k}_1 S_1 + \dot{k}_2 S_2 \\
\frac{dS_1}{dt} &= \dot{b}_1 X_1 \left(S_0 + S_2\right) - \dot{k}_1 S_1 \\
\frac{dS_2}{dt} &= \dot{b}_2 X_2 S_0 - \left(\dot{b}_1 X_1 + \dot{k}_2\right) S_2
\end{aligned}$$

The dynamics of the preferred substrate 1 follow exactly Holling‘s disc equation, as it does not matter whether the unit is in state 0 or state 2, in both cases it will accept an arriving item of type 1. In equilibrium

$$S_1^* = \frac{\dot{J}_1}{\dot{k}_1 + \dot{J}_1}$$

where the arrival rate of substrate 1 is given by $\dot{J}_1 = \dot{b}_1 X_1$.

Noting that $S_0 = 1 - S_1 - S_2$ and setting the third differential equation equal to zero, gives

$$\dot{b}_2 X_2 \left(1 - S_1^* - S_2^*\right) - \left(\dot{b}_1 X_1 + \dot{k}_2\right) S_2^* = 0$$

from which the equilibrium density for state 2 follows

$$S_2^* = \frac{\dot{J}_2(1 - S_1^*)}{\dot{k}_2 + \dot{J}_1 + \dot{J}_2} = \frac{\dot{k}_1 \dot{J}_2}{(\dot{k}_1 + \dot{J}_1)(\dot{k}_2 + \dot{J}_1 + \dot{J}_2)}$$

where $\dot{J}_2 = \dot{b}_2 X_2$.

The product P is delivered with a rate

$$\dot{J}_P = y_1 \dot{k}_1 S_1 + y_2 \dot{k}_2 S_2$$

where y_i gives the number of product particles formed per substrate particle $i = 1, 2$.

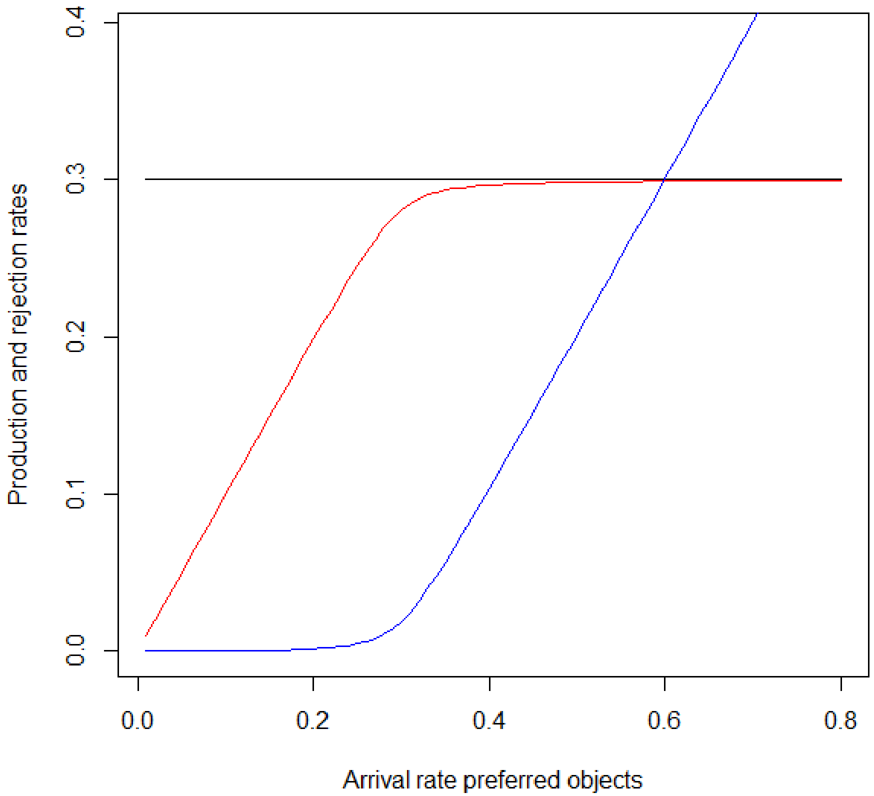

Figure 18: A demand-driven preference SU, with accepted (red line) and rejected (blue line) molecules of the preferred type.

Canonical community model

The canonical ecosystem model is the most simple DEB-based model for V1-morphs, formulated in a mass-mass framework and keeping track of carbon and nitrogen fluxes.

It contains apart from the nutrients carbon dioxide and ammonia, three living (producers, consumers and decomposers) and one non-living group (detritus). Each living group is characterized by a structure and by two (producers) or one (the other two groups) type of reserves. Detritus is split up in 4 types, depending on the origin, which can either be consumer faeces as a result of eating producers, consumer faeces from eating decomposers, consumer dead structure or consumer dead reserves.

The model has therefore 13 state variables. As the system is closed for matter, the dynamics of the nutrients follow automatically from the dynamics of the other 11 state variables.

Table 2: State variables of the canonical ecosystem model. The first letter of the index stands for the type of compound. The second letter stands either for the origin of the faeces or for the group.

Group	Compound	Variable
Detritus	Producer faeces	M_{PP}
Detritus	Decomposer faeces	M_{PD}
Detritus	Dead consumer structure	M_{PV}
Detritus	Dead consumer reserve	M_{PE}
Consumer	Structure	M_{VC}
Consumer	Reserve	M_{EC}
Producer	Structure	M_{VP}
Producer	Reserve 1	M_{E_1P}
Producer	Reserve 2	M_{E_2P}
Decomposer	Structure	M_{VD}
Decomposer	Reserve	M_{ED}
Nutrient	Carbon dioxide	M_C
Nutrient	Ammonia	M_N

Table 3: The flux matrix. Columns refer to state variables, rows to the various processes: A assimilation, G growth, D dissipation, H death, and (second letter) C consumer, P producer and D decomposer.

	PP	PD	PV	PE	VC	EC	VP	E_1P	E_2P	VD	ED
A_1C	+					+	-	-	-		
A_2C		+				+				-	-
GC					+	-					
DC					-	-					
HC			+	+	-	-					
A_1P								+			
A_2P									+		
GP							+	-	-		
DP							-	-	-		
A_1D	-										+
A_2D		-									+
A_3D			-								+
A_4D				-							+
GD										+	-
DD										-	-

Producer SUs

- Three compartments, one structure and two reserves
- Two assimilation SUs: parallel processing
- Two maintenance SUs: demand-driven preference
- One growth SU: parallel processing

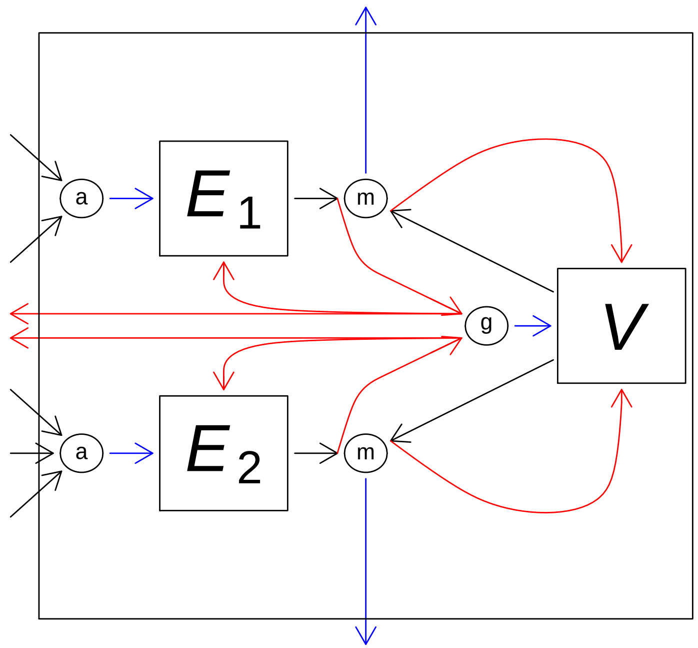

Figure 19: Mass fluxes through the producer. Squares represent the two reserve compartments (E_1 and E_2) and the structural volume (V). Synthesizing units (SUs) are presented by circles.

Parametrization

Consumers are treated as V1-morphs, although most zooplankton and zoobenthos species are actually better characterized as isomorphs.

V1-morph parameters can be derived from isomorph parameters by assuming that all individuals have the same reference structural volume V_d.

The maximum volume-specific assimilation rate can then be obtained from the maximum area-specific assimilation rate as:

$$[\dot{p}_{Am}] = \{\dot{p}_{Am}\}V_d^{-1/3}$$

Similarly, the specific energy conductance parameter $\dot{k}_E$ can be obtained as:

$$\dot{k}_E = \dot{v} V_d^{-1/3}$$

where $\dot{v}$ (cm d^{-1}) is the primary DEB parameter that describes the energy conductance of an isomorph.

Subsequently, the energy-length parameters for V1-morphs can be converted to mass-mass parameters by dividing each volume-specific parameter by the energy density of structure $\mu_E[M_V]$ in J cm^{-3}.

V1 parameters for consumers were derived from isomorphic parameters for $Daphnia\ magna$ available in the add-my-pet library.

We choose the length at puberty as reference structural length ($L_d = V_d^{1/3} = 0.07$ cm) and a value of $\mu_E[M_V]$ equal to 3556 J cm^{-3}.

Model dynamics

- Stable attractor with a one-year period
- Spring and autumn bloom
- Producers start, followed by consumers, detritus and decomposers
- Large fluctuations despite low nitrogen concentration
- Near-zero values may cause numerical problems

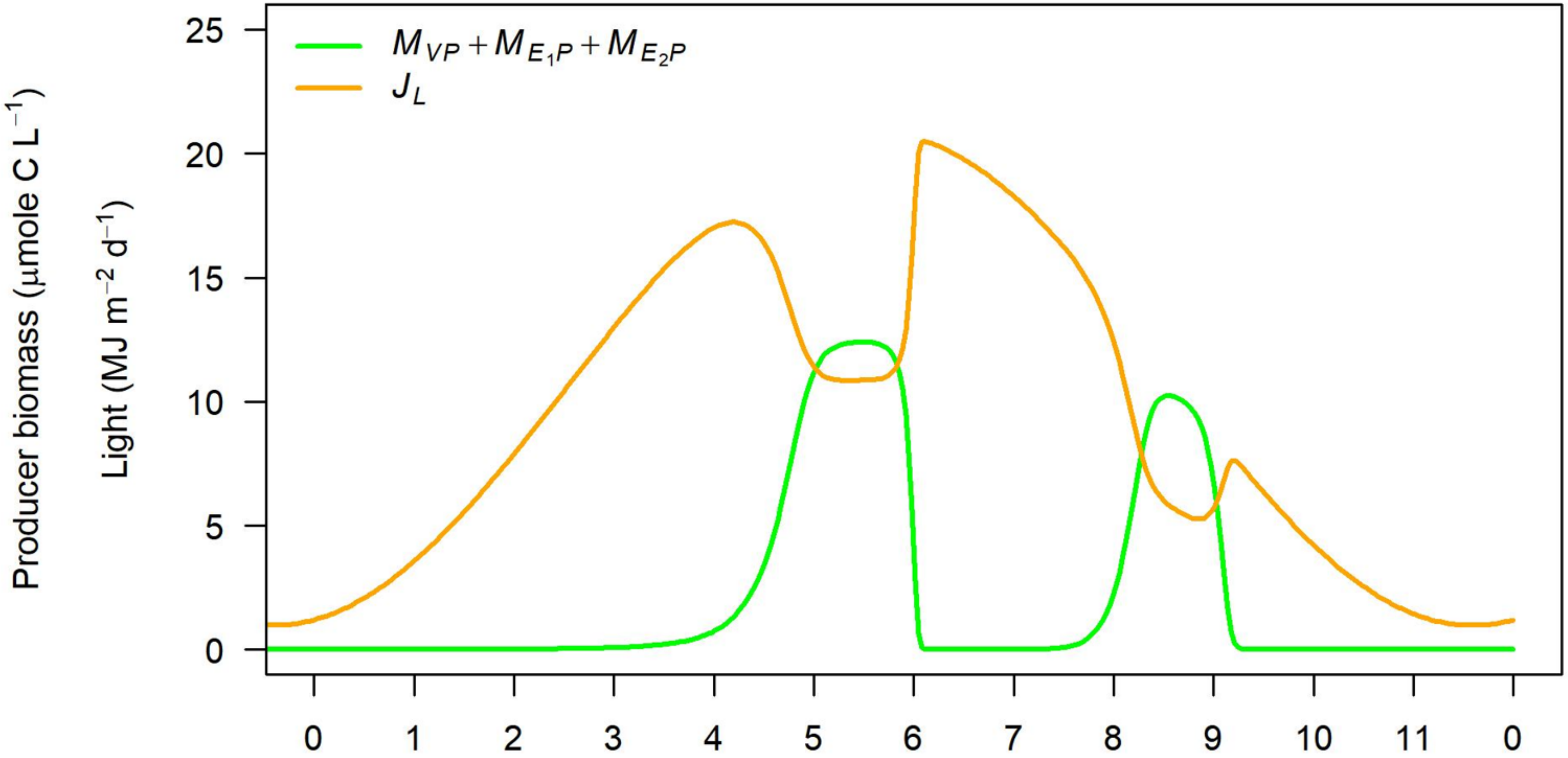

Figure 20: Dynamics of the canonical ecosystem model in the yearly repeating stable attractor. Plotted in the last year of a simulation over 5 years. Light and producer.

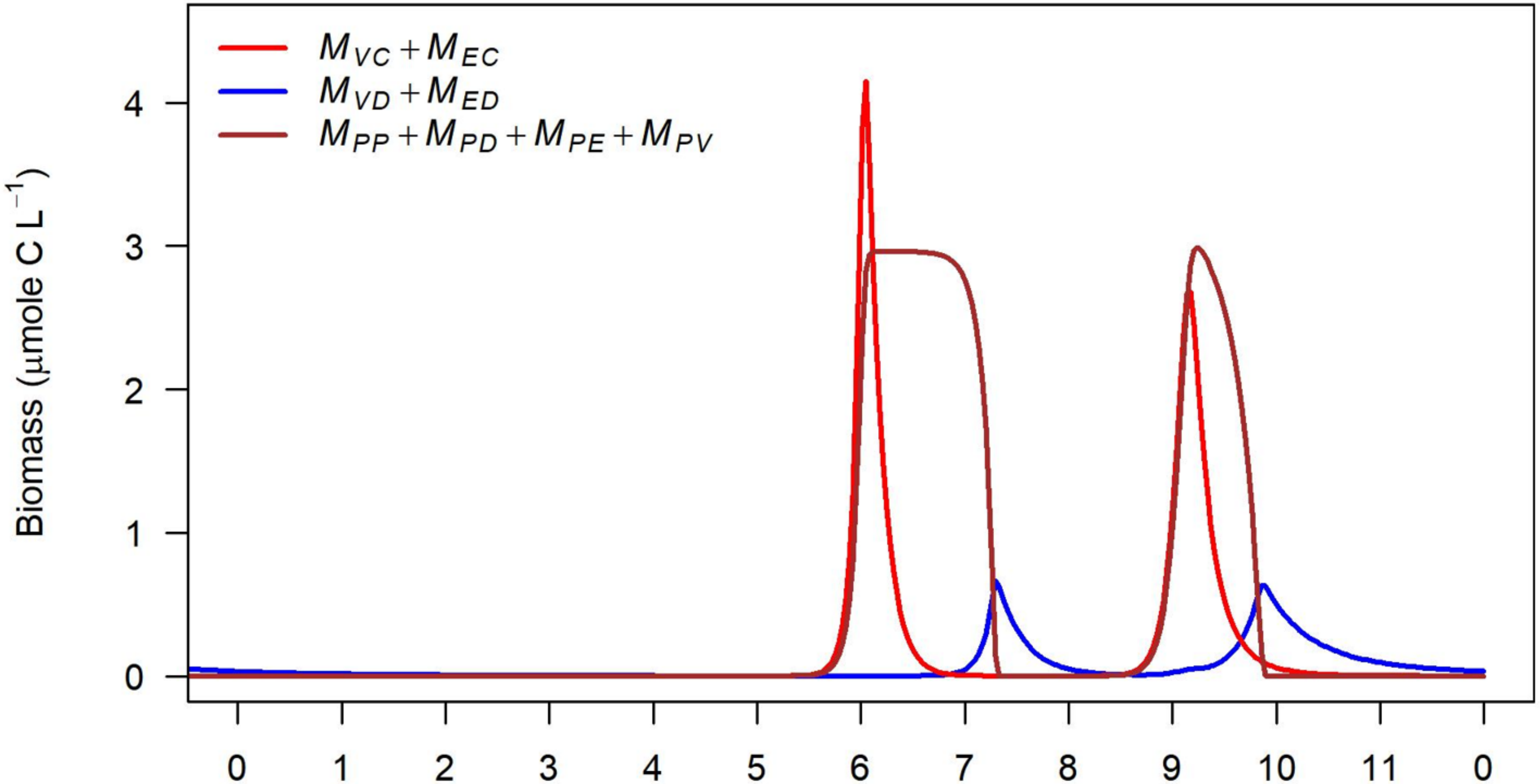

Figure 21: Dynamics of the canonical ecosystem model in the yearly repeating stable attractor. Plotted in the last year of a simulation over 5 years. Consumer, decomposer and detritus.

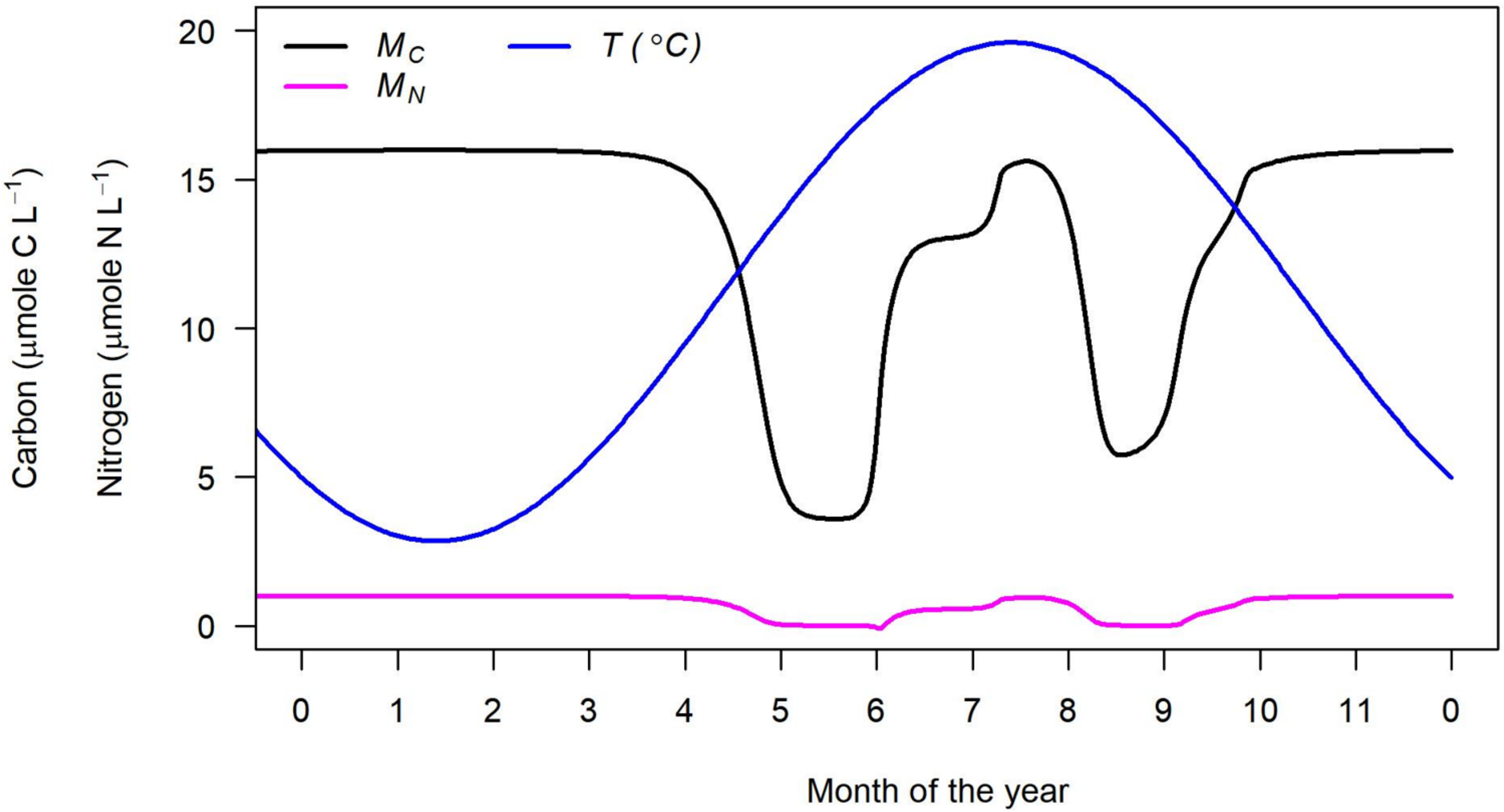

Figure 22: Dynamics of the canonical ecosystem model in the yearly repeating stable attractor. Plotted in the last year of a simulation over 5 years. Temperature and nutrients.

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