# Individual-based and structured population models based on dynamic energy budgets

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# Context

- Many fundamental scientific questions in ecology and ecotoxicolgy relate to the effects of **environmental change** on **populations, communities and ecosystems**.
- These issues are of **critical societal importance**.
- **Pure empiricism** is inadequate.
- **Theory** is required.
- **Dynamics of budgets of energy and elemental matter** should be a component of this theory.

# Mass and Energy Accounting

• A living organism is thermodynamically in a non-equilibrium state, maintained by throughput of energy and elemental matter.

• Energy/mass budgets relate the changes in the state of an individual organism (i-state)of an organism to inputs and outputs.

• Inputs are energy and elemental matter assimilated from the environment (e.g. through food).

• Outputs include eggs, sperm, neonates, seeds, and also abiotic "products" (e.g. feces, $CO_2$ ,$NH_3$) released to the environment.

• **Dynamic Energy Budget** (DEB) models describe how the environment "drives" changes in the state of the organism.

**Energy/mass budgets at different levels of biological organization**

- **Suborganismal**: E/M budgets impact gene expression and physiological/biochemical rates.
- **Individual Organism**: E/M budgets relate "performance" (growth, development, reproduction) to environment.
- **Population**: E/M budgets influences changes in population over time (*qualitative*: stability, cycles and *quantitative*: population size, age and size structure).
- **Community**: E/M budgets may impact biodiversity (debatable)
- **Ecosystem**: Focus on energy and material flows among *groups of species* (e.g. trophic levels).

DEB theory aims to relate processes at the different levels, but starts with a representation of *individual* budgets.

# Aims of lecture

1) Introduce Dynamic Energy Budget (DEB) theory

2) Describe demography based on a DEB model

3) Introduce (with applications) DEB-based “structured” population models written as:

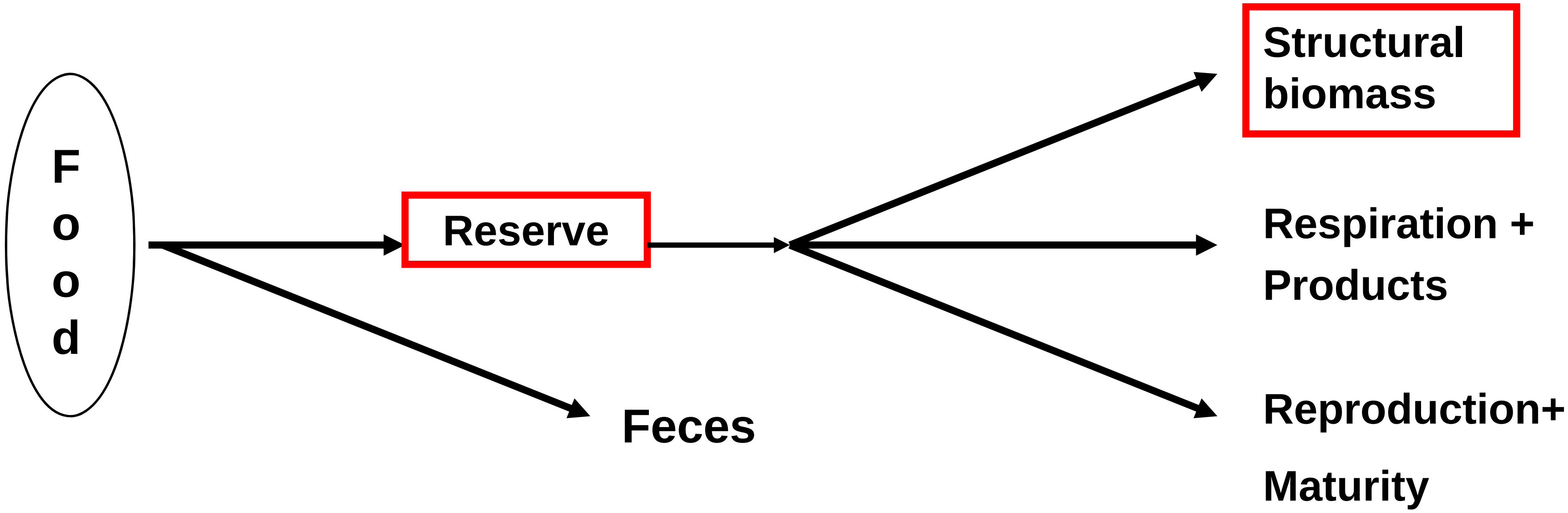
- ordinary differential equations
- delay-differential equations

4) DEB-based individual-based models (IBMs)* (with application)

* DEB-IBM exercise available

# Dynamic Energy Budget models

# Sloppy representation of Kooijman's DEB model*



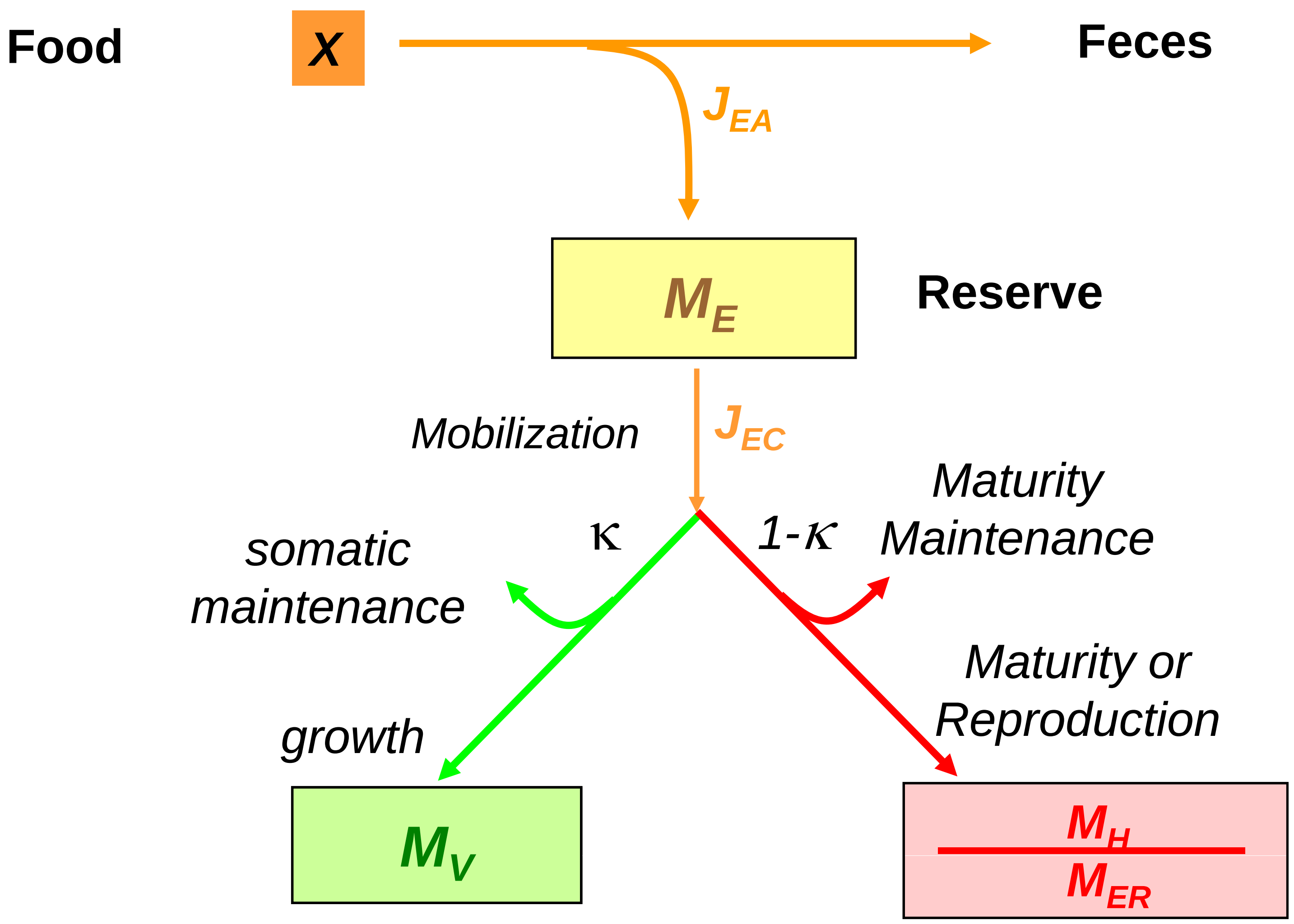

***Key Ingredients:***

Structure: biomass that requires maintenance.

Reserve: biomass that can be mobilized for metabolic processes

- S.A.L.M. Kooijman *Dynamic Energy Budgets for Metabolic Organization*. Cambridge University Press, 2010
- Lectures by R. Nisbet: http://www.cein.ucla.edu/new/p156.php?pageID=367

# Kooijman's "standard" DEB model



# Kooijman's "standard" DEB model*

***i*-state variables**

- **Reserve biomass** at time *t*
- **Structural biomass** at time *t*
- "**Cumulative reproduction**", i.e. total carbon allocation to reproduction buffer by time *t*
- Total allocation to "**maturity**" by time *t* .
- **Hazard rate** at time *t*, i.e. instantaneous "risk" of mortality
- **Aging acceleration** at time *t* – related to level of damage inducing compounds

**Parameters**

Total of ~12 parameters. Of these some are expected to be broadly invariant across taxa and others scale in predictable way with size. This opens the way to generality. For many applications, fewer state variables and parameters suffice.


S.A.L.M. Kooijman (2010) Dynamic Energy Budget models for metabolic organization. Cambridge University Press.
T. Sousa et al (2010)., *Philosophical Transactions of the Royal Society B*, **365**:3413-3428.

# Kooijman's "standard" DEB model equations

$$\frac{d}{dt}M_E = \dot{J}_{EA} - \dot{J}_{EC}$$

$$\frac{d}{dt}M_V = \dot{J}_{VG} = (\kappa \dot{J}_{EC} - \dot{J}_{EM})y_{VE}$$

$$\frac{d}{dt}M_H = (1-\kappa)\dot{J}_{EC} - \dot{J}_{EJ} \quad \text{if } M_H < M_H^p \quad \text{, else } \frac{d}{dt}M_H = 0$$

$$\frac{d}{dt}M_{ER} = 0 \quad \text{if } M_H < M_H^p \quad \text{, else } \frac{d}{dt}M_{ER} = (1-\kappa)\dot{J}_{EC} - \dot{J}_{EJ}$$

with $\dot{J}_{EA} = c(T)\, f\{\dot{J}_{EAm}\}L^2 \quad \text{if } M_H \geq M_H^b \quad \text{else } \dot{J}_{EA} = 0$

$$\dot{J}_{EC} = c(T)\{\dot{J}_{EAm}\}L^2 \frac{ge}{g+e}\left(1+\frac{L}{gL_m}\right)$$

$$\dot{J}_{EM} = c(T)[\dot{J}_{EM}]L^3$$

$$\dot{J}_{EJ} = c(T)\dot{k}_J M_H$$

PLUS ODEs for aging acceleration and hazard rates

# Kooijman's "standard" DEB model equations

**COLLECTION OF MESSY ODEs**

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$$\frac{d}{dt}M_R = 0 \text{ if } M_H < M_H^p \text{ else } \frac{d}{dt}M_R = (1-\kappa)\dot{J}_{EC} - \dot{J}_{EJ}$$

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PLUS ODEs for aging acceleration and hazard rates

# DEB-based Population Dynamics

# First…a little demography

Consider a population of females divided into **discrete age classes**

Let $S_a$ be the fraction of newborns that **survive** to age $a$

Let $\beta_a$ be the total **number of offspring** from individual aged $a$ .

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Then the average number of female offspring expected in a lifetime is

$$R_0 = \sum_{\substack{\text{all age} \\ \text{classes}}} \beta_{\mathrm{a}} S_a$$

This quantity is called **net reproductive rate** in many ecology texts
(N.B. not a rate)

In **continuous time** $R_0 = \int_0^\infty \beta(a) S(a) da$ (changing summation → integral)

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In **standard DEB**, we can compute $\beta(a)$ and $S(a)$ by solving a system of 6 differential equations for a constant environment. Then we can compute $R_0$.

# A little population ecology

- Ultimate fate of a closed population that does not influence its environment is **unbounded growth** or **extinction**.

- Without feedback, the long-term average pattern of growth or decline of populations is **exponential** – even in fluctuating environments

- The **long term rate of exponential growth**, *r*, is obtained as the solution of the "Euler-Lotka" equation[1]

$$1 = \int_0^\infty \beta(a) S(a) e^{-ra} da$$

(Note similarity to equation for $R_0$ )

- **Feedback** from organisms in focal population to the environment may lead to an **equilibrium population** ($R_0 = 1$) or to more exotic population dynamics such as cycles.

1. A.M. de Roos (*Ecology Letters* 11: 1-15, 2009) contains a computational approach (with sample code) for solving this equation when $\beta(a)$ and $S(a)$ come from a DEB model.

# Application: response of mussels to ZnO NPs[1,2]

Adult marine mussels, *Mytilus galloprovincialis*, were exposed to ZnO NPs for 12 weeks at concentrations up to 2 mg $L^{-1}$.

Basic measurements on individuals(2 food levels)

1) weights of shell, gonad, somatic tissue
2) Zn distribution within organism
3) Tank clearance rates → information on food consumed.
4) Iindividual clearance rates
5) Oxygen consumption rates.

used to estimate toxicity parameters

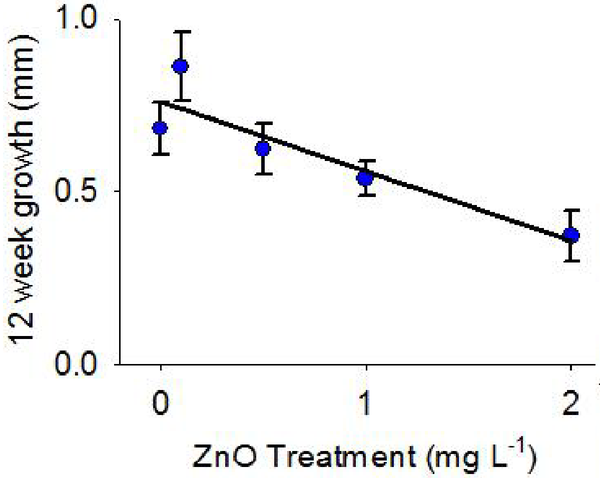
Population level prediction

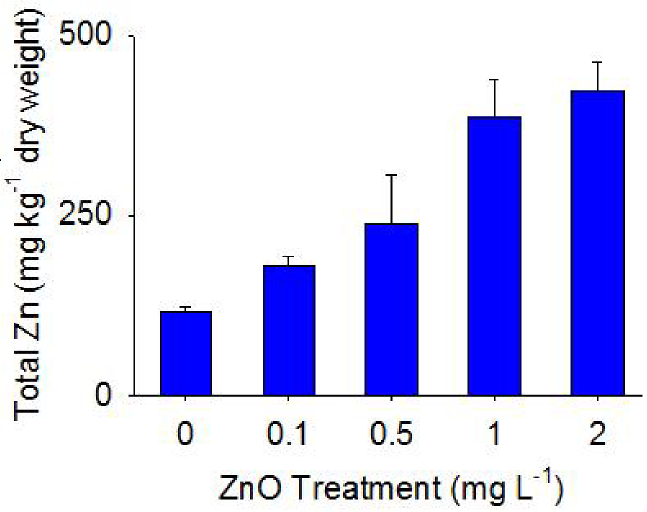
$$R_0 = \int_0^\infty \underbrace{\beta(a)}_{\text{fecundity at age } a} \underbrace{S(a)}_{\text{survival to age } a} da$$

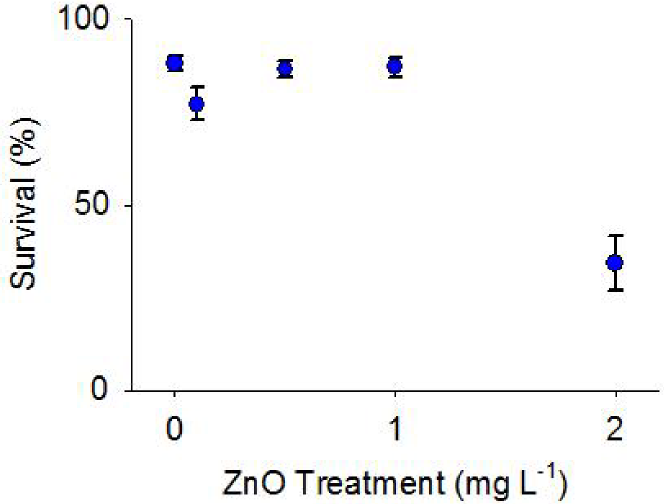
From DEB model


1. S. Hanna et al . *PLoS ONE*, **8** (4), e61800 (2013)
2. E.B. Muller et al. *Journal of Sea Research*, submitted

# 12 week exposure of *M. galloprovincialis* to ZnO NPs

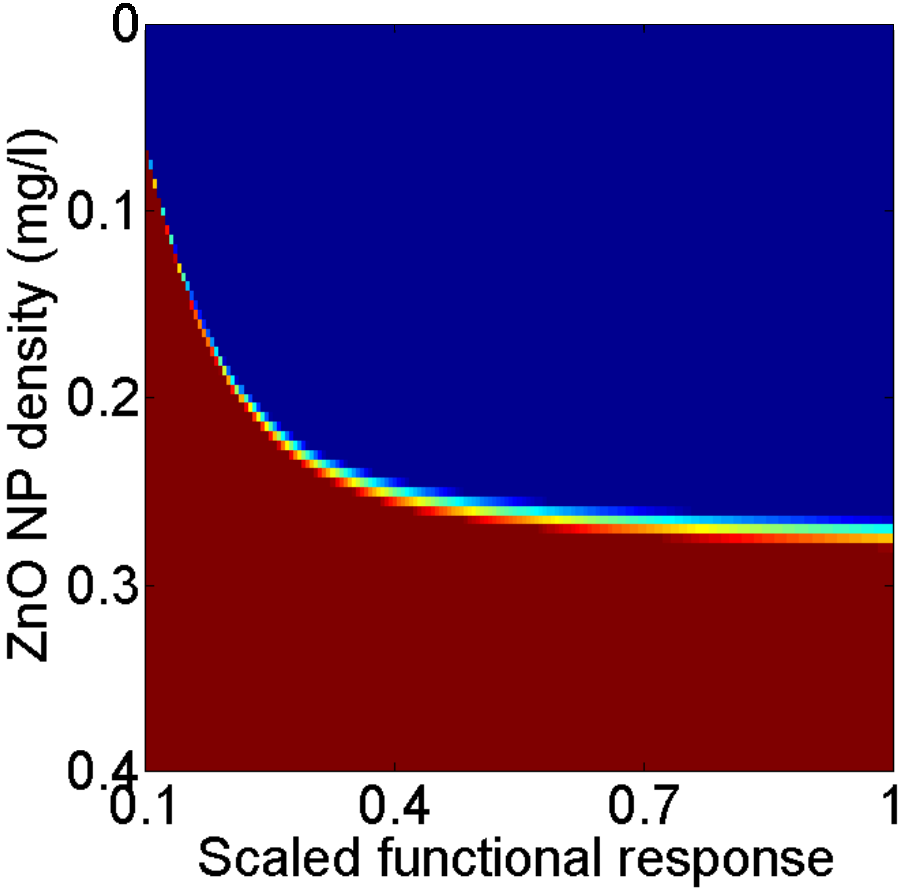



- ZnO NPs inhibit mussel growth with increasing concentrations but may promote growth at low levels
- Mussels accumulate Zn in soft tissue when exposed to ZnO NPs
- Survival of mussels decrease at 2mg $L^{-1}$ ZnO NPs

# $EC_{50}$ EXPECTED LIFE-TIME PRODUCTION OF REPRODUCTIVE MATTER




- **$EC_{50}$ for a given food level**

- **MUCH SMALLER THAN FOR INDIVIDUAL RATES (e.g. 1.5 mg/l for feeding)**

# Incorporating feedback from organisms to environment

# Simplest approach: use ordinary differential equations or delay differential equations for p-state dynamics

**ODEs** can be derived with "*ontogenetic symmtery*"[1]

1) All physiological rates proportional to biomass (in biomass budget models) or to structural volume (in DEB models)
2) All organisms experience the same per capita risk of mortality (hazard)
3) Include ODEs describing environment (E-state)

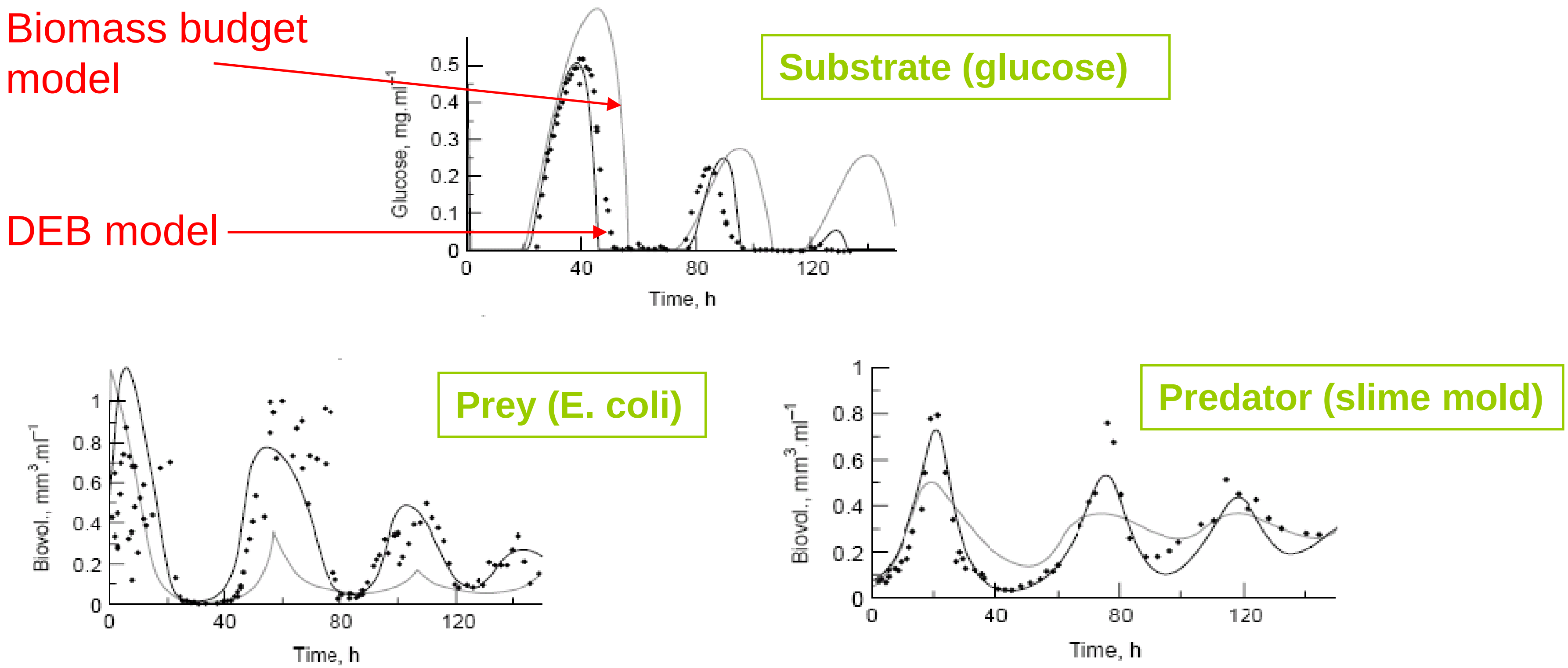
Resulting equations describe biomass dynamics

**Delay differential equations (DDEs)** follow if assumption 2 is relaxed to[2,3]:

2a) All organisms *in a given life stage* experience the same risk of mortality


1. A.M. de Roos and L.Persson (2013). *Population and Community Ecology of Ontogenetic Development*. Princeton University Press. See also lectures by de Roos: http://www.science.uva.nl/~aroos/Research/Webinars
2. R.M. Nisbet. Delay differential equations for structured populations. Pages 89-118 *in* S. Tuljapurkar, and H. Caswell, editors. *Structured Population Models in Marine, Terrrestrial, and Freshwater Systems.* Chapman and Hall, New York.
3. Murdoch, W.W., Briggs, C.J. and Nisbet, R.M. 2003. *Consumer-Resource Dynamics*. Princeton University Press.

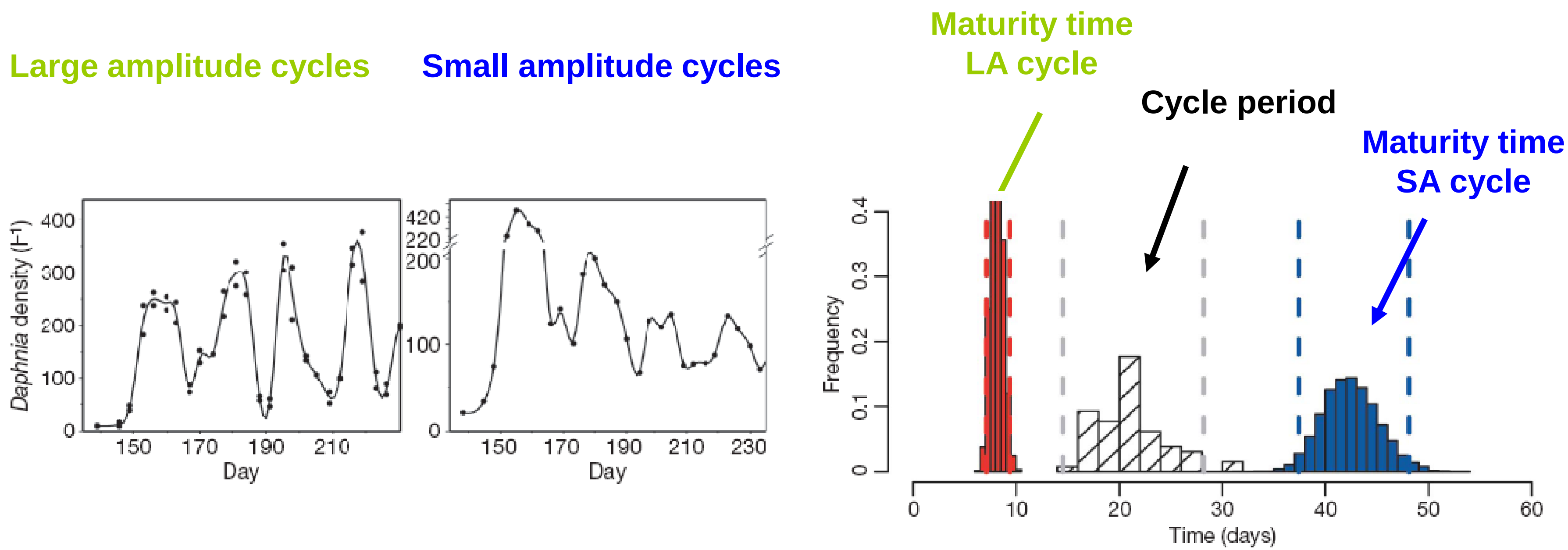
# Application of ODEs: A DEB-based ODE model (with reserves) describes observed cycles in microbial populations





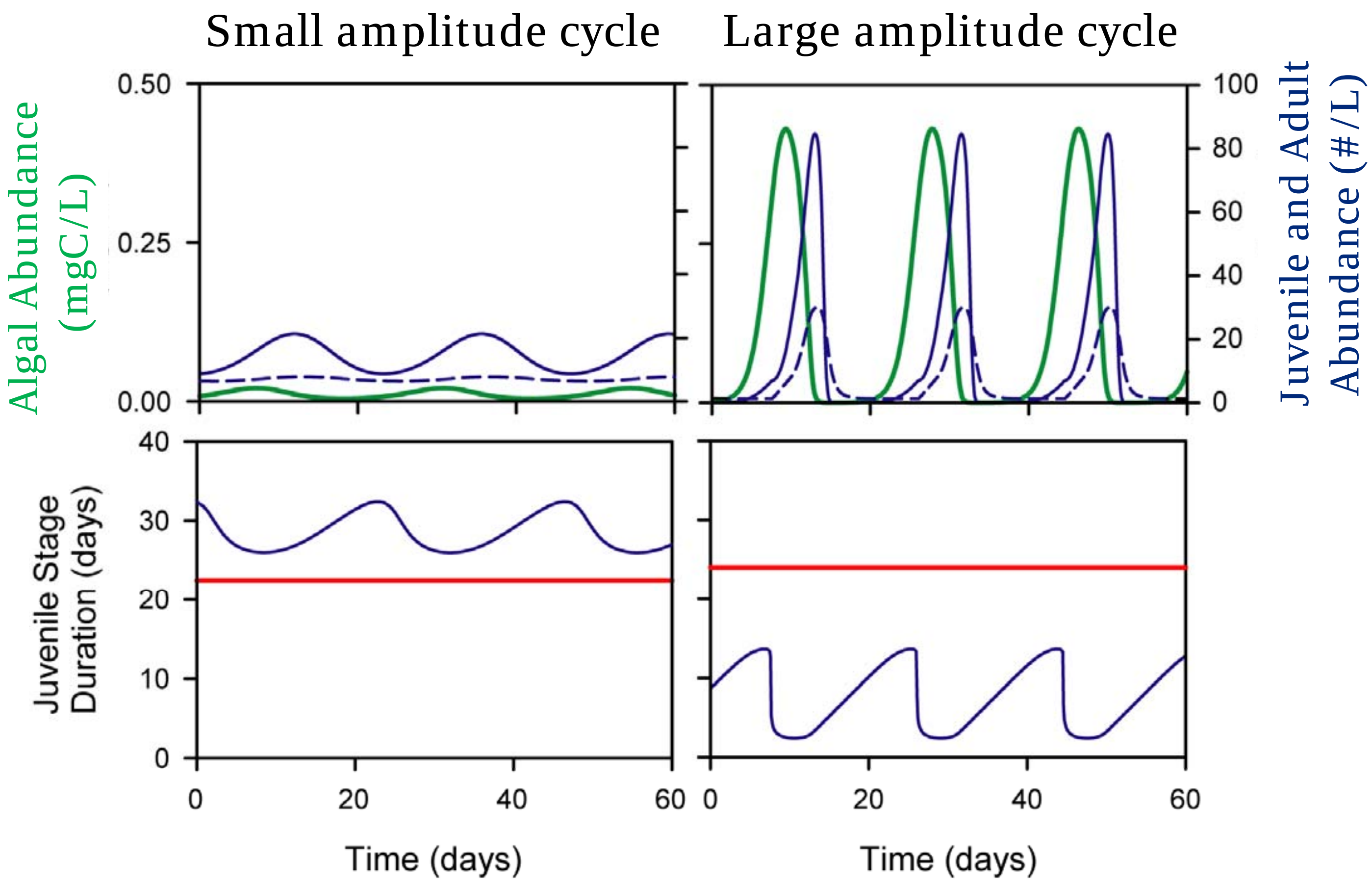
1. R.M. Nisbet et al. J. Anim. Ecol. 69: 913-926, 2000

# A DDE model describes Daphnia populations in large lab systems*




* McCauley, E., Nelson, W.A. and Nisbet, R.M. 2008. Small amplitude prey-predator cycles emerge from stage structured interactions in *Daphnia*-algal systems. *Nature*, **455**: 1240-1243.

# DDE model

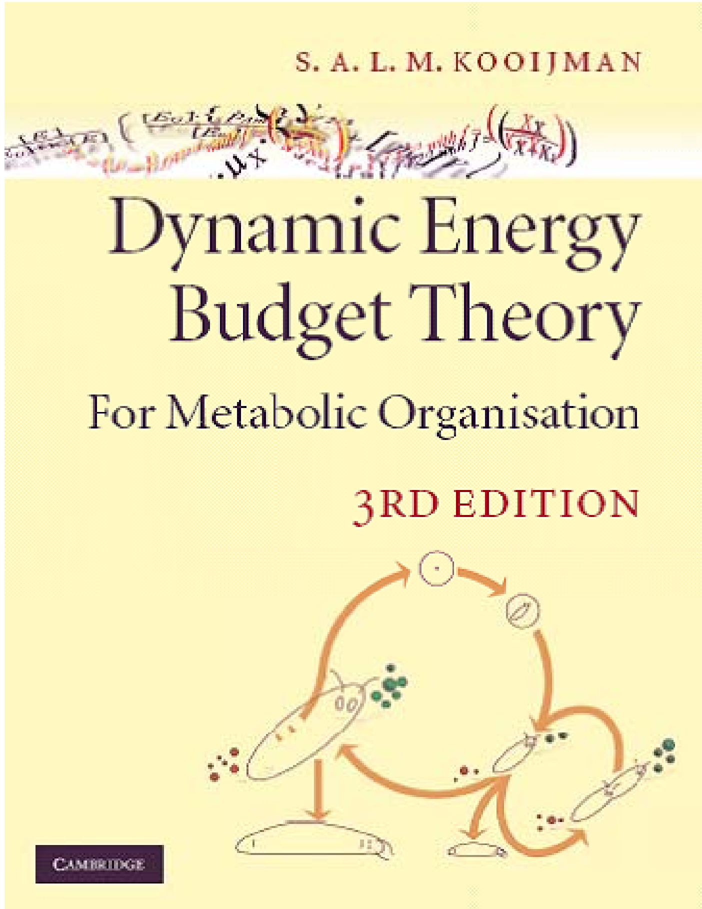


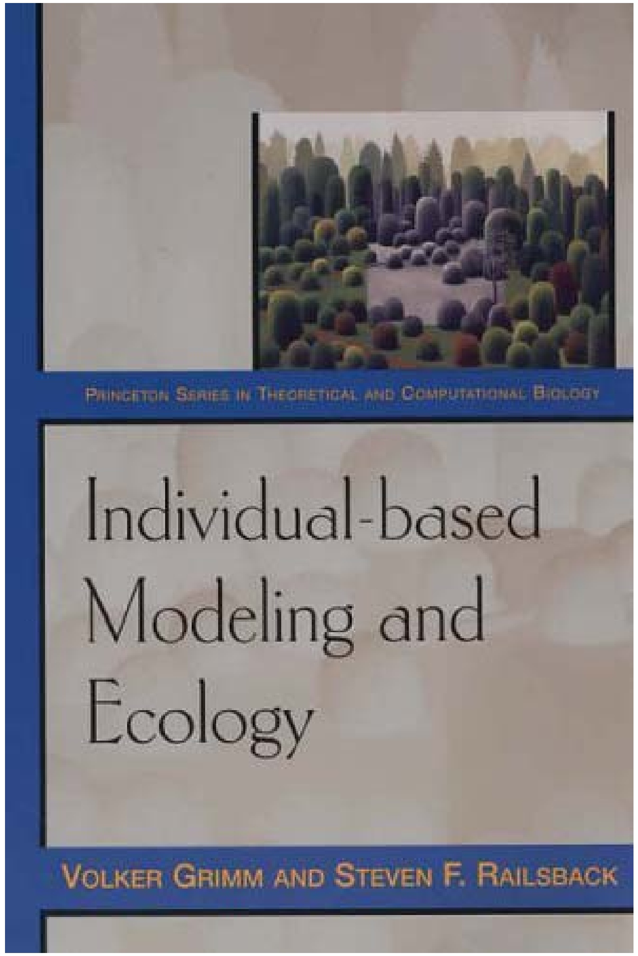

- Key feature absent from standard DEB: food-dependent juvenile mortality

# Individual or agent based population models (IBMs)*

* Many thanks to Ben Martin for collaboration and slides on IBMs

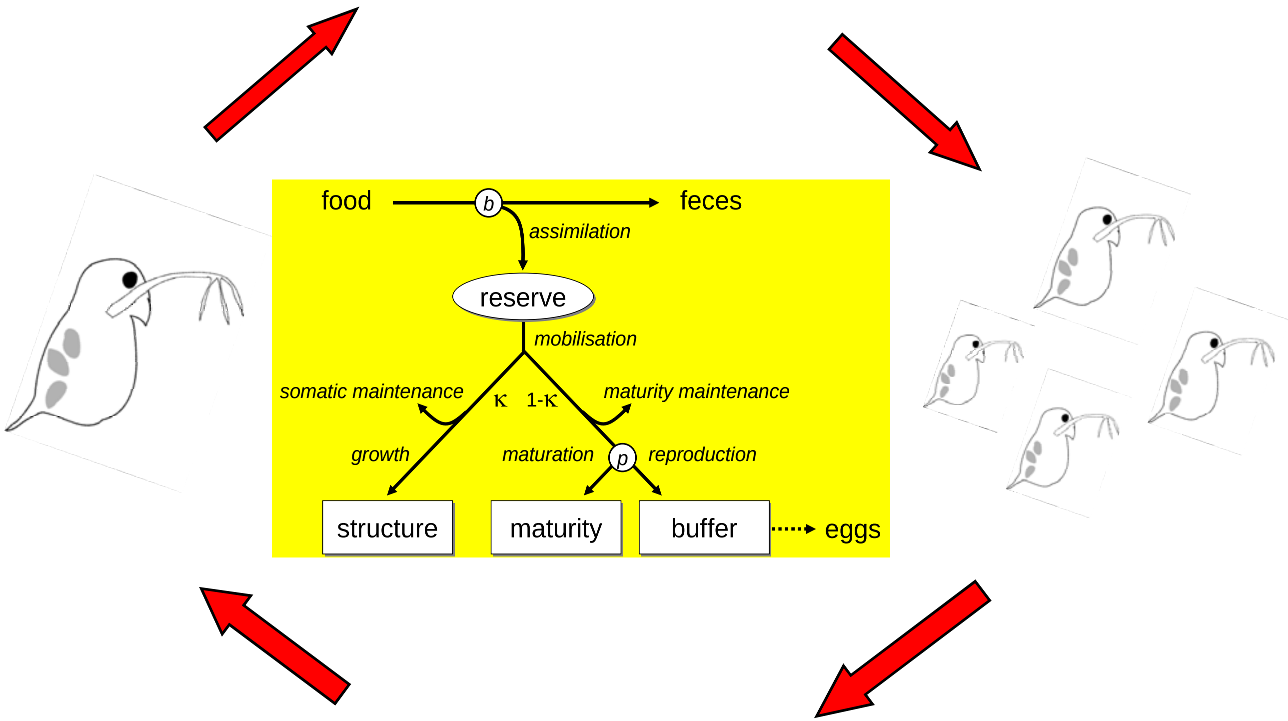
# DEB-based IBMs*




* B.T. Martin, E.I. Zimmer, V.Grimm and T. Jager (2012). *Methods in Ecology and Evolution* 3: 445-449

# DEB-IBM

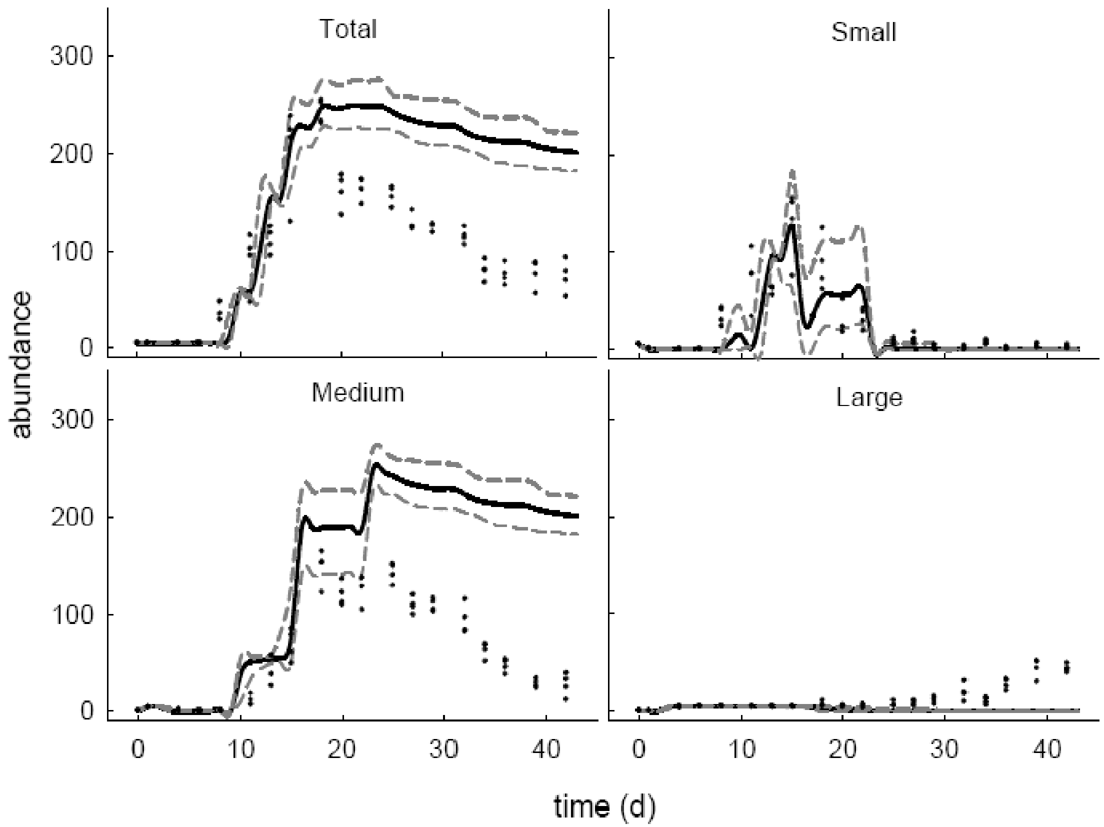



- Implemented in *Netlogo* (Free)
- Compute population dynamics in simple environments with minimal programming
- User manual with examples

# DEB-IBM display

# Population model tests*

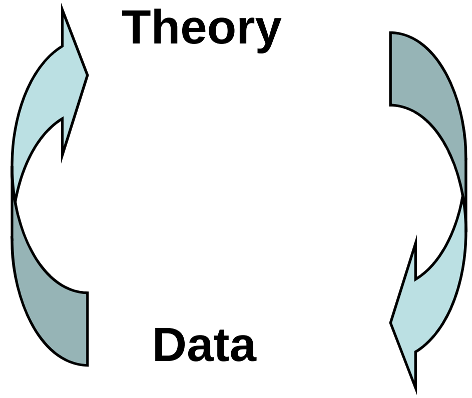
**Low food (0.5mgC $d^{-1}$)**



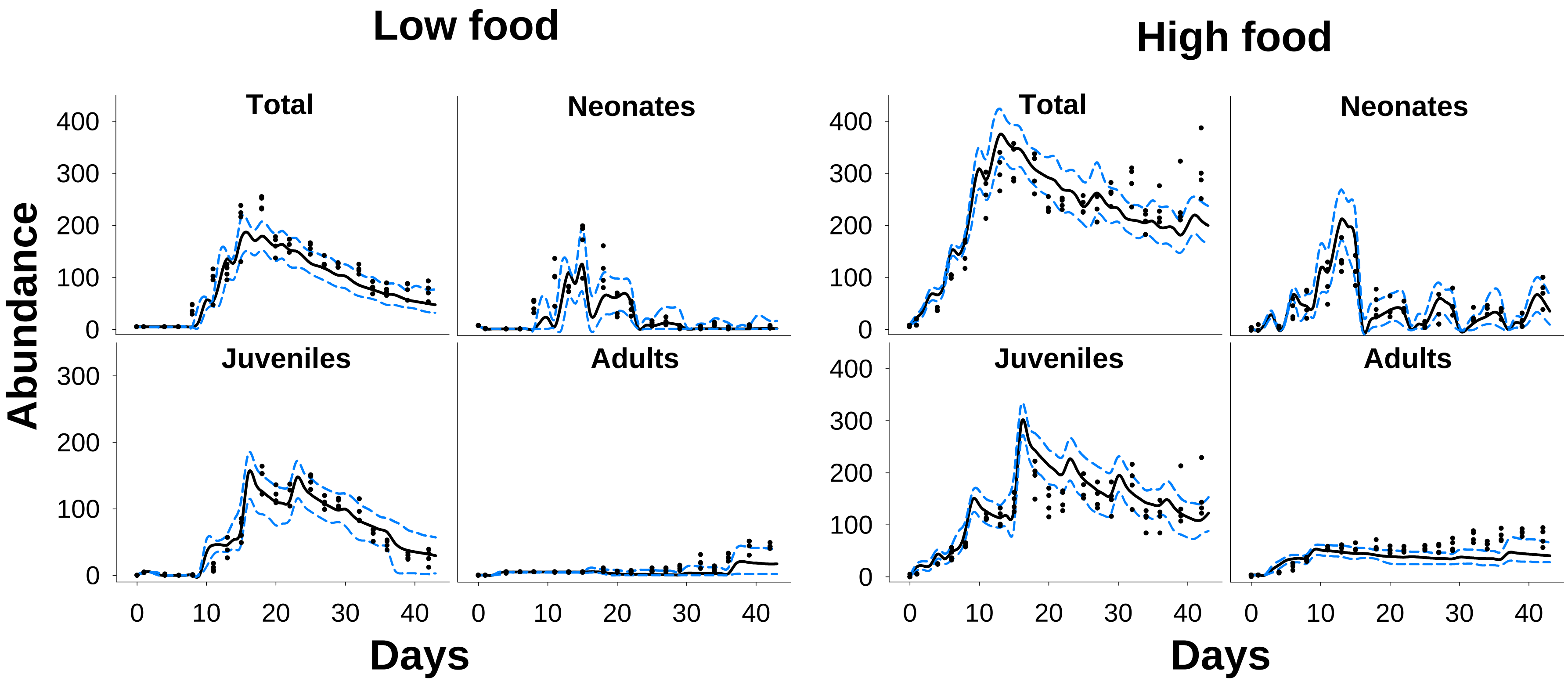

* B.T. Martin, T. Jager, R.M. Nisbet, T.G. Preuss, V. Grimm(2013). Predicting population dynamics from the properties of individuals: a cross-level test of Dynamic Energy Budget theory. *American Naturalist*, **181**:506-519.

# Refining the model

- Martin et al. tested 3 size selective food-dependent submodels
    - Juveniles more sensitive
    - Adults more sensitive
    - Neutral sensitivity
- Fit submodels to low food level compare GoF at all food levels

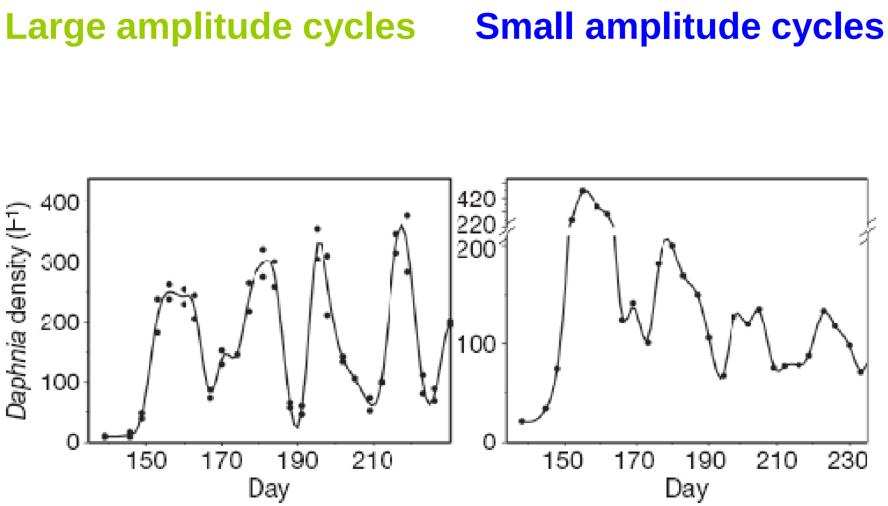


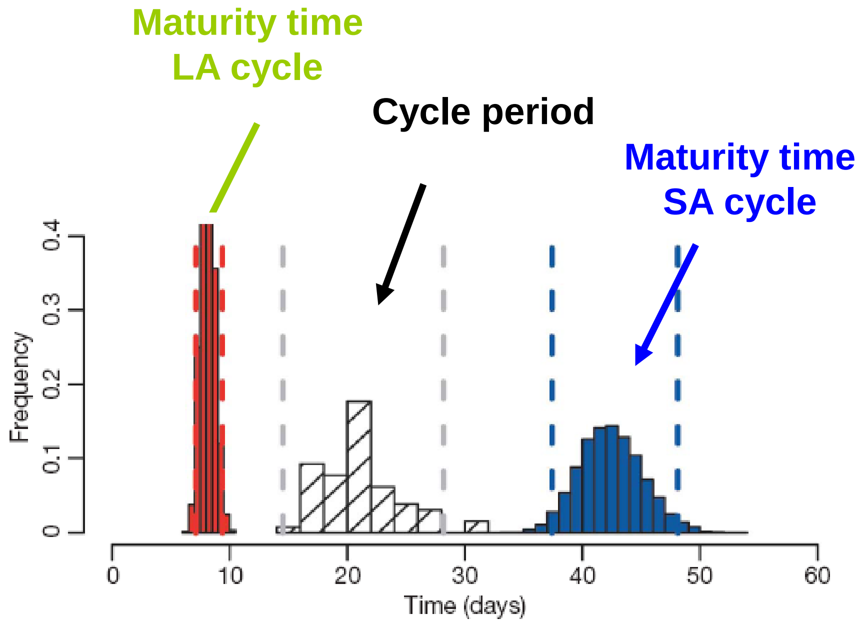
# Best model



Low food
High food
Total
Neonates
Juveniles
Adults
Abundance
Days
0
100
200
300
400
0
10
20
30
40

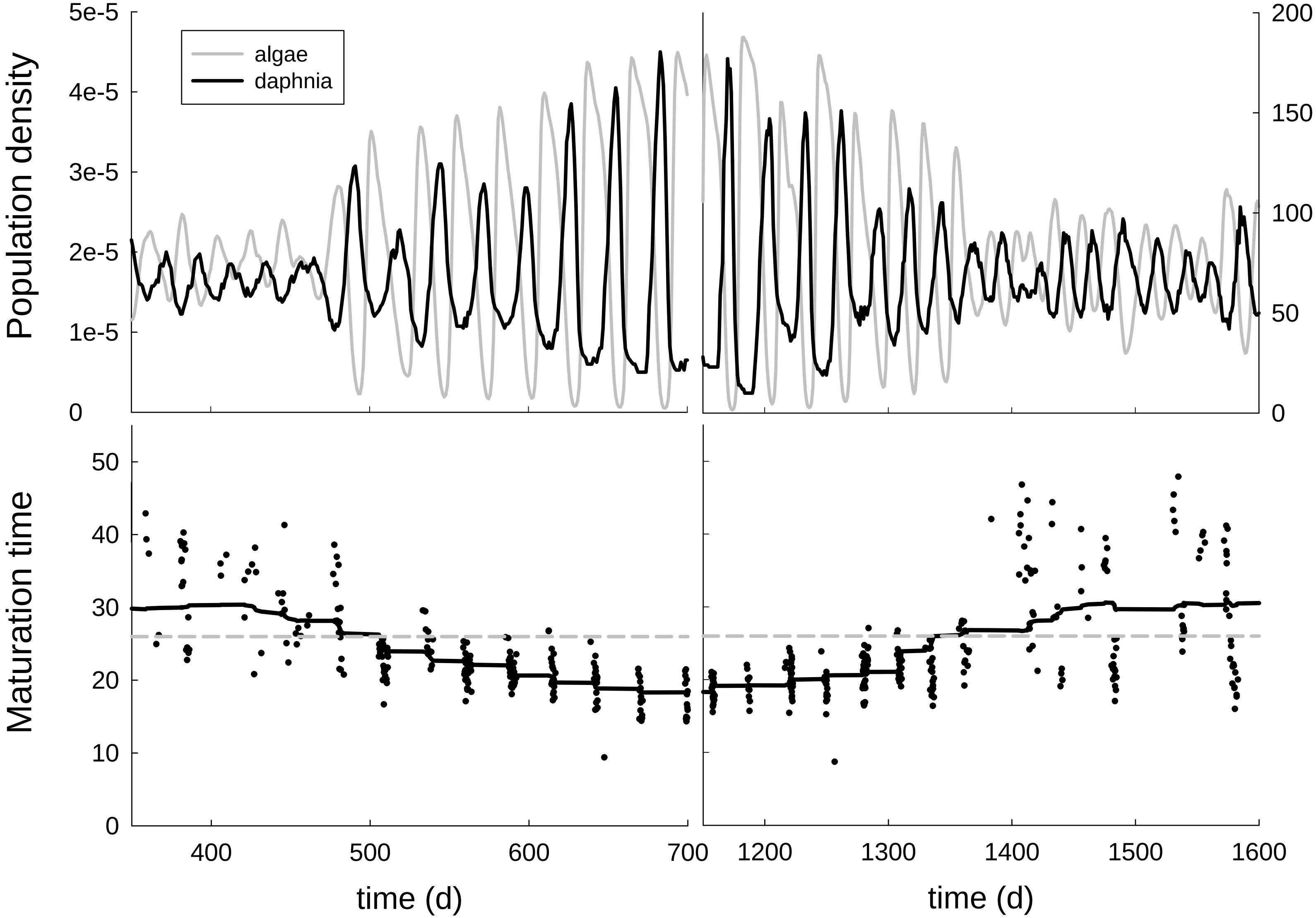
# Futher test: Daphnia populations in large lab systems*



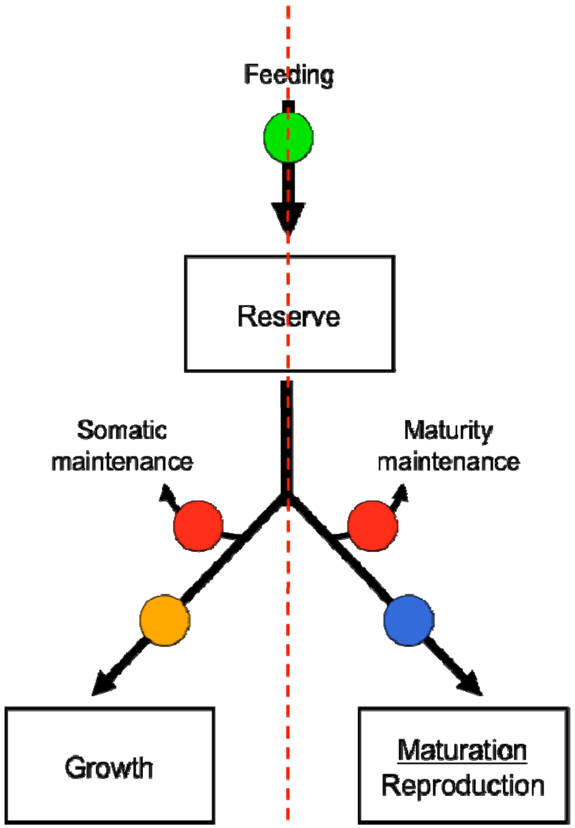



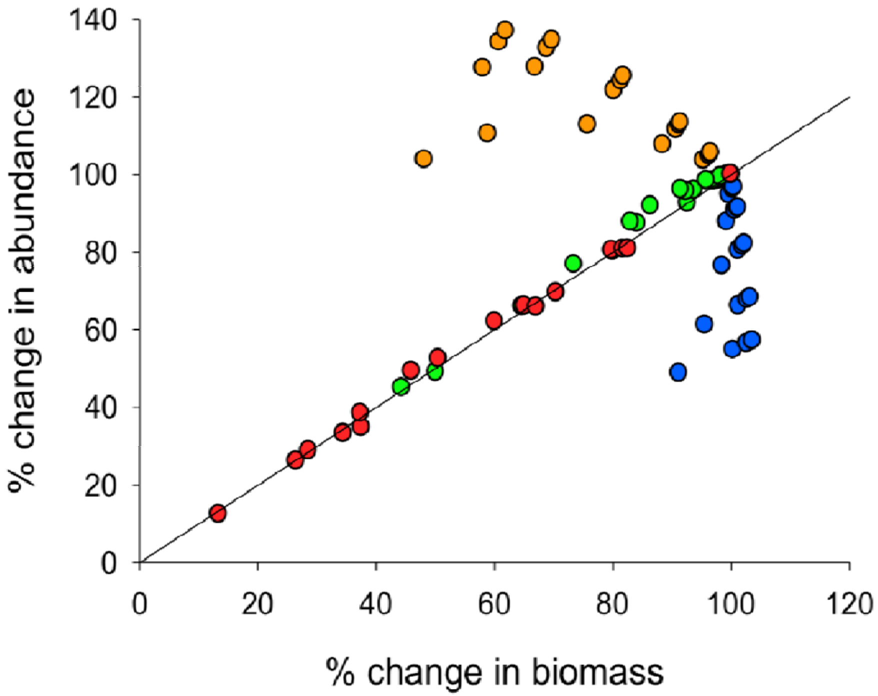

* McCauley, E., Nelson, W.A. and Nisbet, R.M. 2008. Small amplitude prey-predator cycles emerge from stage structured interactions in *Daphnia*-algal systems. *Nature*, **455**: 1240-1243.

# DEB-IBM dvnamics



Further application: relating physiological mode of action of toxicants to demography of populations near equilibrium[1]




1. Martin, B., Jager, T., Nisbet, R.M., Preuss, T.G., and Grimm, V, *submitted*.

# Take Home Messages on population dynamics

- With no feedback from organisms to their environment, a population will ultimately grow or decline exponentially.
- Exponential growth rate can be calculated from DEB model of complete life cycle.
- With feedback, describing population dynamics requires either an individual-based or a structured population model. Good software available for both.
- With very special assumptions, structured population models reduce to a system of ODEs or DDEs.
- DEB-IBM results may be consistent with previous size-structured models – gives support for both.

# Aims of lecture

1) Introduce Dynamic Energy Budget (DEB) theory

2) DEB-based demography

3) DEB-based "structured" population models:
   - ordinary differential equations

   - delay-differential equations

4) DEB-based individual-based models (IBMs)

# Aims of lecture

1) Introduce Dynamic Energy Budget (DEB) theory

2) DEB-based demography
   Mussels exposed to nanoparticles

3) DEB-based "structured" population models:
   - ordinary differential equations
     Microbial chemostat
   - delay-differential equations
     Daphnia population dynamics

4) DEB-based individual-based models (IBMs)
   Daphnia (again)
   Ecotoxicology of populations at equilibrium