



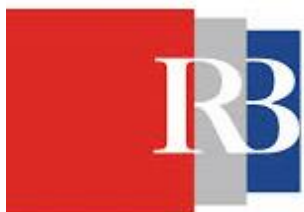
DEB modules and applications

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Bošković*



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University of Crete, Heraklion, Greece
deb2025.sciencesconf.org

Outline

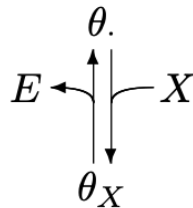
- Feeding-digestion modules
 - Use of SUs
 - Gut passage
- Reproduction modules
 - Batch spawning
 - Feeding upregulation
- Starvation modules
 - Shrinking
 - Rejuvenation
- Trajectory reconstruction
 - Through fitting
 - Through model inversion

1. Feeding - digestion

Feeding/Digestion - iso 111

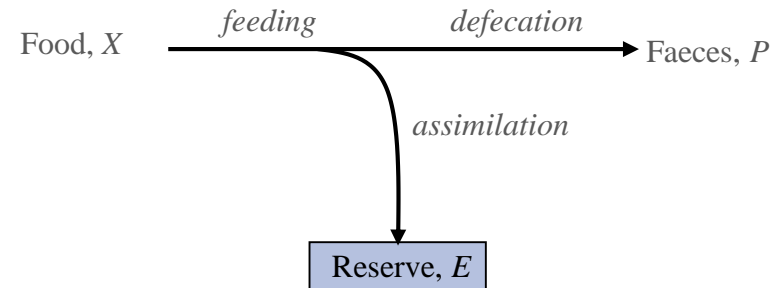
Standard module of food uptake

make product E from a single substrate X
food searching and food handling



Dynamics of the fractions θ of the SUs at different states:

$$\begin{aligned}\frac{d\theta.}{dt} &= -y_{EX}j_X\theta. + \dot{k}\theta_X \\ \frac{d\theta_X}{dt} &= y_{EX}j_X\theta. - \dot{k}\theta_X \\ \theta. + \theta_X &= 1\end{aligned}$$



$$j_{EA} = \dot{k} \theta_X^* = \frac{1}{\dot{k}^{-1} + (y_{EX}j_X)^{-1}}$$

$$j_{EA} = \dot{k} \frac{X}{X + \dot{k}(y_{EX}\theta_X)^{-1}}$$

j_* Flux of the substrate

y_{EX} Yield coefficient

\dot{k} metabolic/handling processing

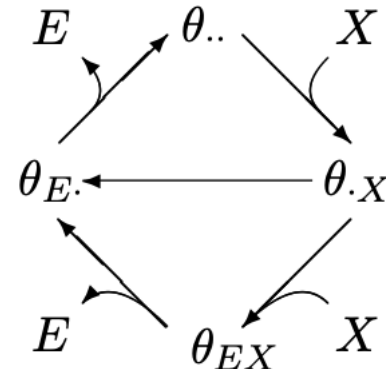
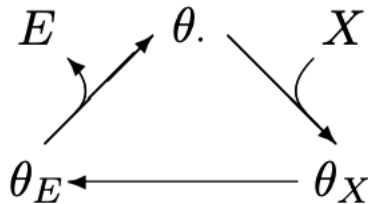
Extensions

DEB3 Chapter 7.2.2



Food handling is partitioned in mechanical and metabolic handling

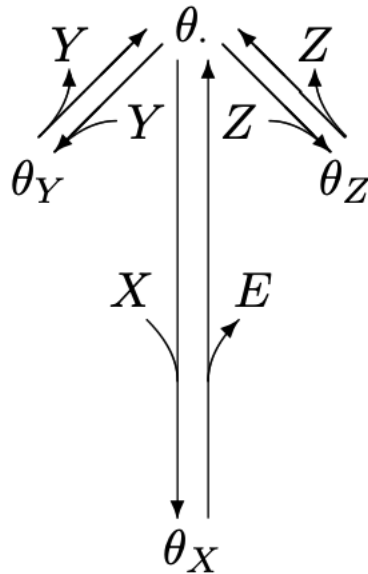
- metabolic handling follows mechanical handling (**sequential**)
- food searching can be **parallel** to metabolic handling



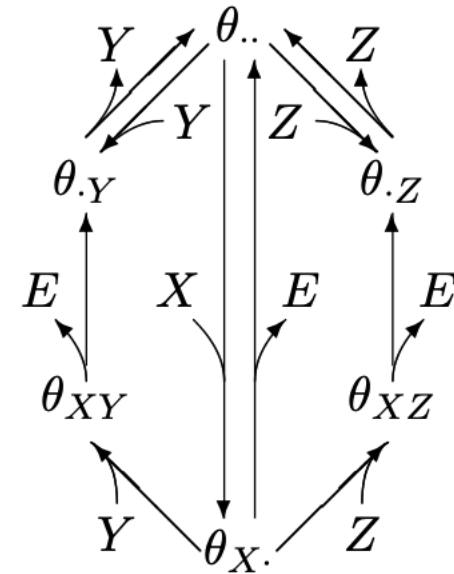
Applied to feeding data for sea bream *Sparus aurata* larvae

Lika & Papandroulakis (2005) Can. J. Fish. Aquat. Sci. 62: 425–435

Social interaction DEB3 7.2.4



Food processing sequential to socialisation



Food processing parallel to socialisation

Example: SUs and pseudofaeces in bivalves

Journal of Sea Research 62 (2009) 72–74



Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares



Effect of food quality on energy uptake

Jeffrey S. Ren

National Institute of Water and Atmospheric Research, PO Box 8602, Christchurch, New Zealand



2006). To improve its applicability, Kooijman (2006) extended the functional response to include an inorganic term, as

$$J_x = \frac{\{J_{xm}\} \cdot V^{2/3} \cdot X}{K(Y) + X} \quad \text{with } K(Y) = K \cdot (1 + Y / K_Y)$$





In Collaboration with the
Royal Netherlands Institute
for Sea Research

Journal of Sea Research 56 (2006) 103–106

**JOURNAL OF
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www.elsevier.com/locate/seares

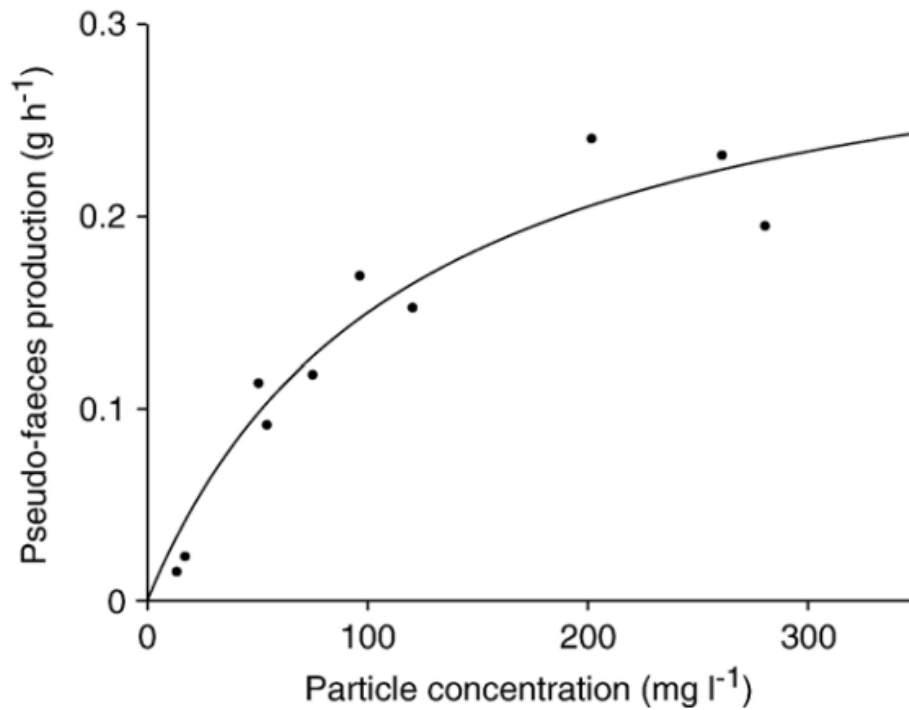


Pseudo-faeces production in bivalves

S.A.L.M. Kooijman

Department of Theoretical Biology, Vrije Universiteit, de Boelelaan 1087, 1081 HV Amsterdam, the Netherlands

Available online 30 March 2006





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Pseudo-faeces production in bivalves

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Available online 30 March 2006

Pseudo-faeces production (g h⁻¹)

0.3
0.2

$\delta_{YX}=1$. The maximum filtering rate is at $X=0$, $Y=0$,
so

$$F_m = F(0, 0) = \frac{J_{Xm}}{K} = \frac{k_X k_D N_A N_D}{k_X N_A - k_D N_D} \frac{(k_X N_A - k_D N_D) b_X}{k_X k_D N_D}$$

$$= N_A b_X$$

$$F(X, Y) = \frac{\{F_m\} V^{2/3}}{1 + Y/K_Y + X/K}$$

$$J_X = N_A \theta_X^A * b_X X = N_D \theta_X^D * k_D$$

$$= \frac{k_X k_Y k_D N_A N_D b_X X}{k_X k_Y k_D N_D + (k_X N_A - k_D N_D) k_Y b_X X + k_D N_D k_X b_Y Y}$$

$$J_Y = N_A \theta_Y^A * b_Y Y = N_A \theta_Y^A * k_Y$$

$$\theta_X^A * = k_X k_Y k_D N_D / \Theta$$

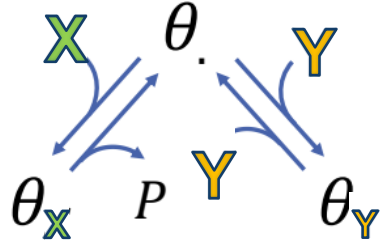
$$\theta_Y^A * = k_Y b_Y X (k_Y N_A - k_D N_D) / \Theta$$

$$+ k_D N_D k_X b_Y Y$$

$$(k_X k_Y - k_Y b_X X + k_X b_Y Y).$$

Plastic ingestion



$$\frac{d\theta}{dt} = -\dot{b}_{XX}\theta + k_{XX}\theta_X - \dot{b}_{YY}\theta + k_{YY}\theta_Y$$


$$\frac{d\theta_X}{dt} = \dot{b}_{XX}\theta - k_{XX}\theta_X$$

$$\frac{d\theta_Y}{dt} = \dot{b}_{YY}\theta - k_{YY}\theta_Y$$

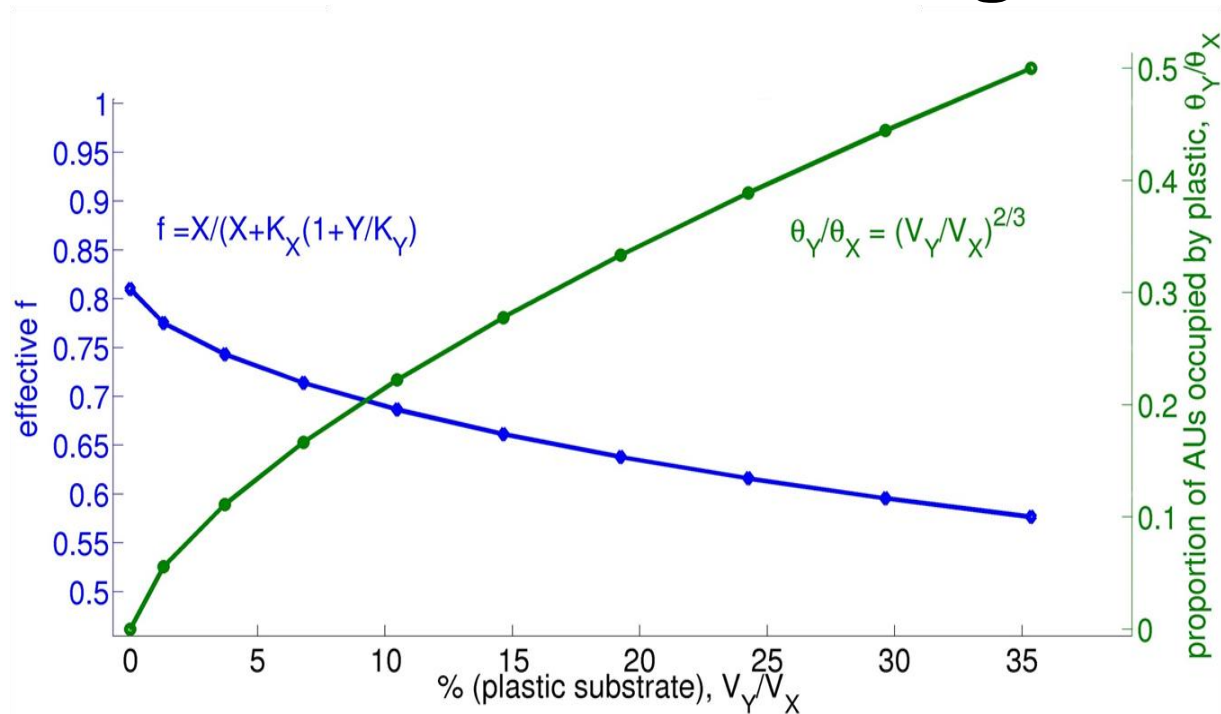
$$J_{EA} = V^{2/3} \underbrace{\{J_{Xm}\}}_{\{J_{Am}\}} y_{EX} \theta_X^* + V^{2/3} \{J_{Ym}\} y_{EY} \theta_Y^*$$

equal to zero as plastic substrate has no digestible energy, $y_{EY}=0$

$$\theta_X^* = \frac{X}{X + K_X(1 + Y/K_Y)}$$

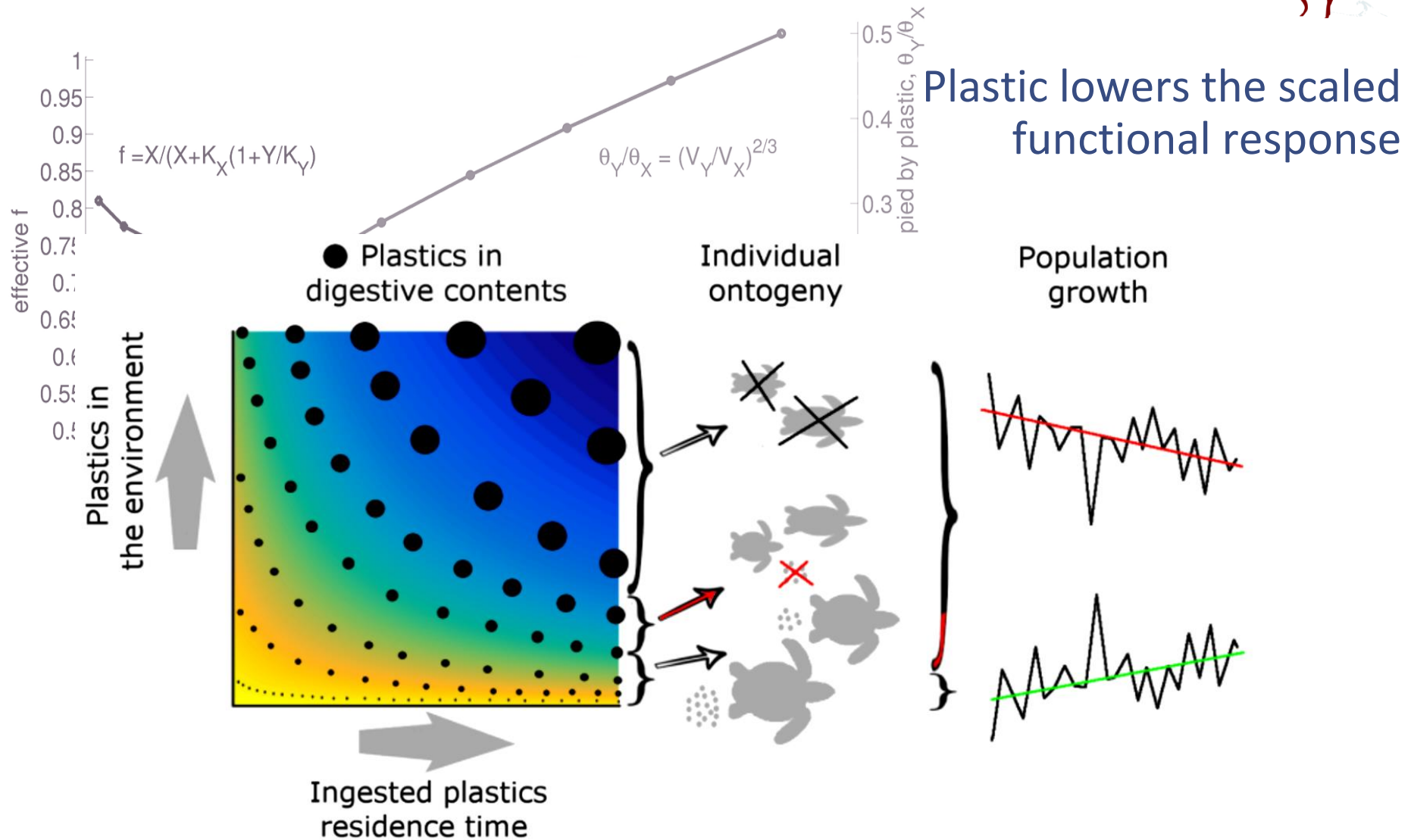
effective f (functional response)

Plastic ingestion



Plastic lowers the scaled functional response

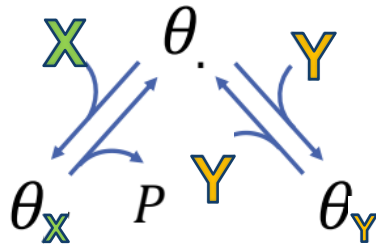
Plastic ingestion



Multiple substrates



$$\frac{d\theta}{dt} = -\dot{b}_{X\theta} \theta + k_{X\theta} \theta_X - \dot{b}_{Y\theta} \theta + k_{Y\theta} \theta_Y$$



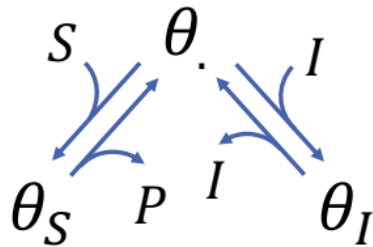
$$\frac{d\theta_X}{dt} = \dot{b}_{X\theta} \theta - k_{X\theta} \theta_X$$

$$\frac{d\theta_Y}{dt} = \dot{b}_{Y\theta} \theta - k_{Y\theta} \theta_Y$$

Inhibition



$$\frac{d\theta}{dt} = -\dot{b}_S S \theta + \dot{k}_S \theta_S - \dot{b}_I I \theta + \dot{k}_I \theta_I$$



$$\frac{d\theta_S}{dt} = \dot{b}_S S \theta - \dot{k}_S \theta_S$$

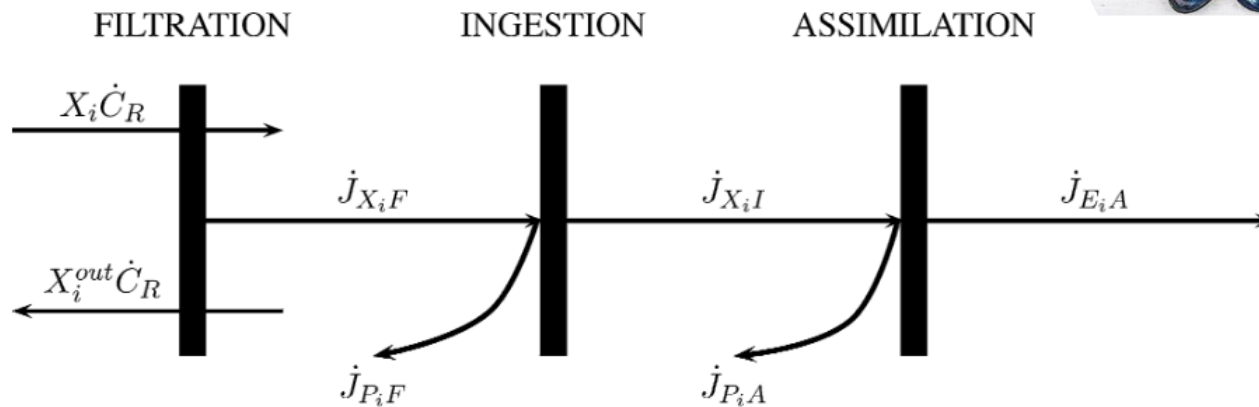
$$\frac{d\theta_I}{dt} = \dot{b}_I I \theta - \dot{k}_I \theta_I$$

Multiple relevant processes and substrates (Bivalves)



S. Saraiva et al. / Ecological Modelling 222 (2011) 514–523

515



*(Turtles are less complicated than bivalves!)

Saraiva et al. 2011, Eco mod

Feeding – iso 221 DEB3 comments 5.2.7

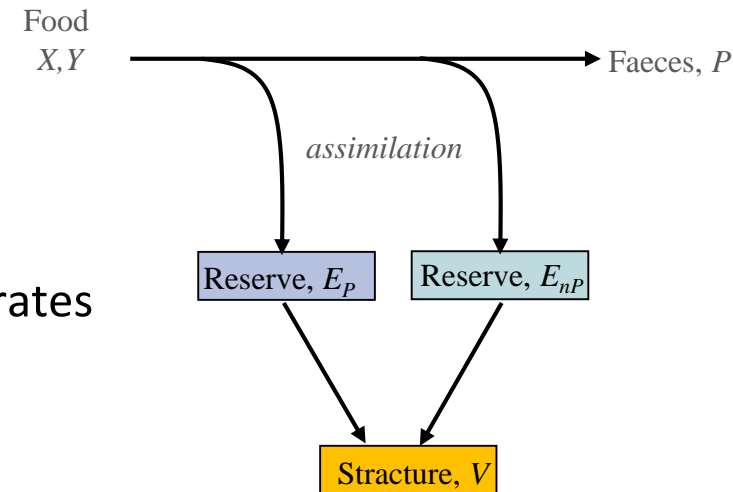
Extension of the standard DEB model for

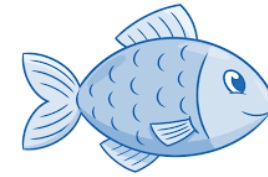
2 types of food X and Y of constant composition
sequential processing of substitutable substrates

2 reserves
protein standing for 'building block' reserve
non-protein for energy reserve
each food type contributes to both reserves

1 structure

Somatic maintenance is paid from protein and non-protein reserves (substitutable), with a strong preference for non-proteins, and the binding is parallel.

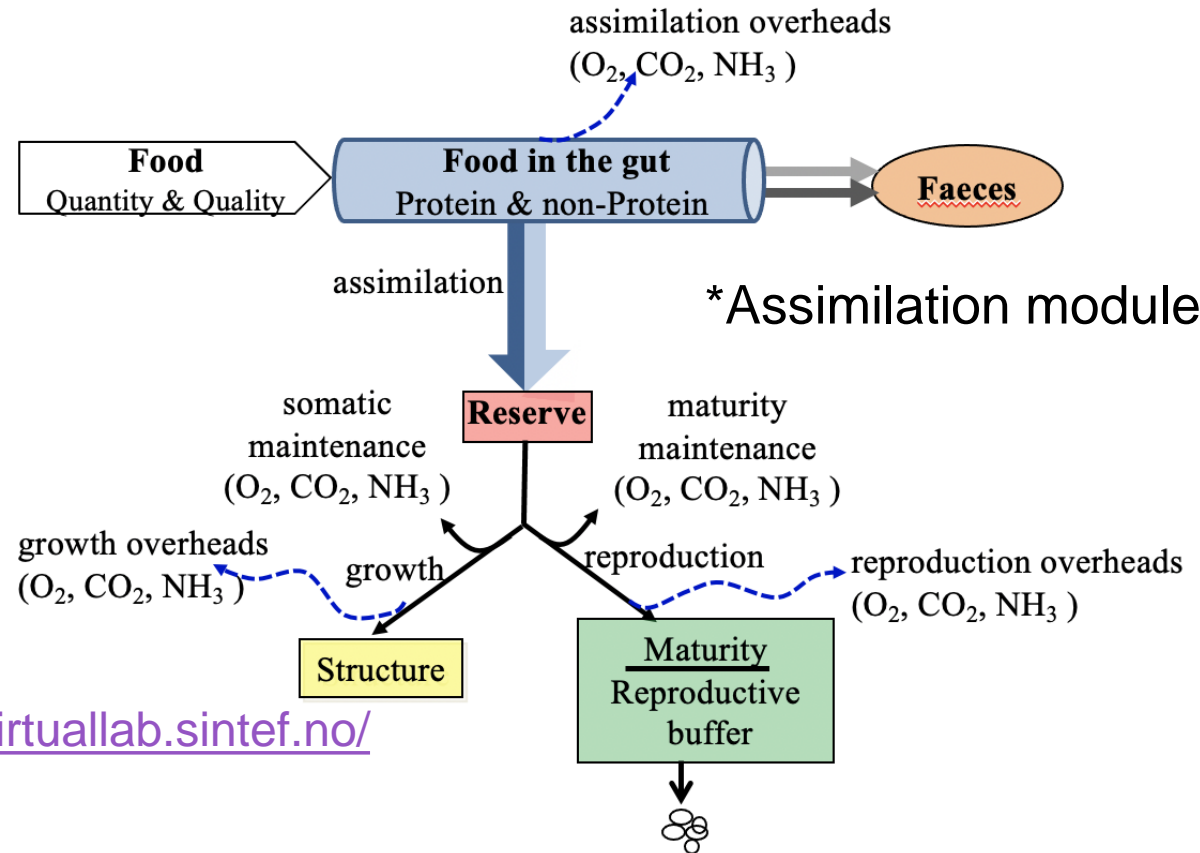




Nutritional bioenergetics model

State variables

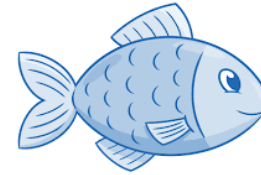
- Food in the gut (M_X)
- Reserve energy (E)
- Structural body volume (V)
- Energy investment into maturation (embryos, juveniles) (E_H)
- Energy allocated to reproduction (adults) (E_R)



A **VL** system to test in silico different experimental protocols, before the real implementation in the research facility.

Note: check for project update (AquaExcel3.0) : <https://aquaexcel.eu/>

Assimilation module



Assimilation rate

Depends on the mass of food in the stomach-gut

Proportional to the surface of the gut wall

Depends on the fraction of protein and lipid in the food

$$\dot{J}_{EA} = \left\{ \dot{J}_{EA_m} \right\} f L^2$$

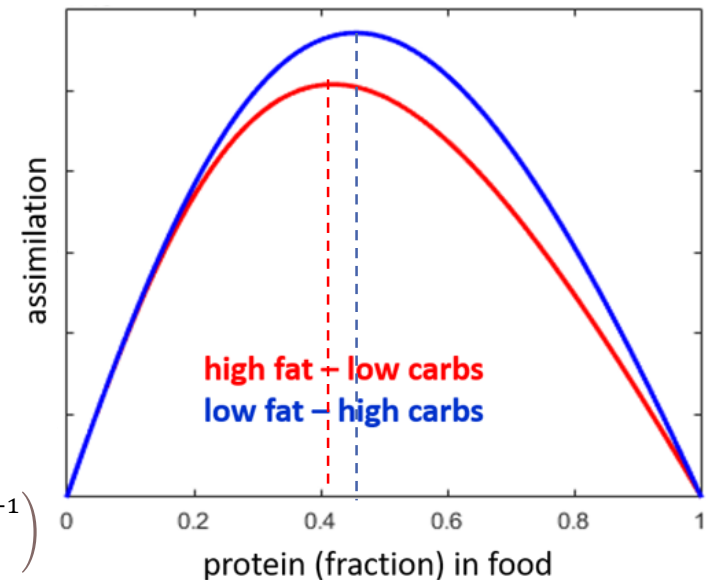
$$f = \frac{M_X}{M_X + M_K^X}$$

$$M_K^X = \frac{\left\{ \dot{J}_{EA_m} \right\}}{\left\{ \dot{J}_{Xg_m} \right\}} \left(\left(y_{EX_P} a_P \right)^{-1} + \left(y_{EX_{nP}} (1 - a_P) \right)^{-1} - \left(y_{EX_P} a_P + y_{EX_{nP}} (1 - a_P) \right)^{-1} \right)$$

Effects of food composition on assimilation



Effects of protein-energy (PE) ratio in the diet



2. Reproduction

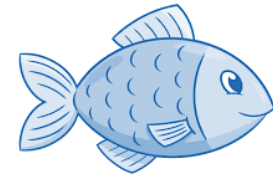
Reproduction

Reserve allocated to reproduction is collected in a reproduction buffer.

Handling rules for the conversion of the buffer's energy to eggs or foetuses are species-specific (e.g. batch vs. single offspring, cueues etc):

- Can include extra state variables.
- Often depend on environmental variables, the energy status (of the organism or the reproduction buffer itself), hormones, or some combination.

Reproduction handling rules



Example for multiple-batch spawners

Reproduction rate

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

Rate of batch preparation

$$\dot{p}_B = \kappa_R((1 - \kappa)\dot{p}_{Cm} - \dot{p}_J)$$

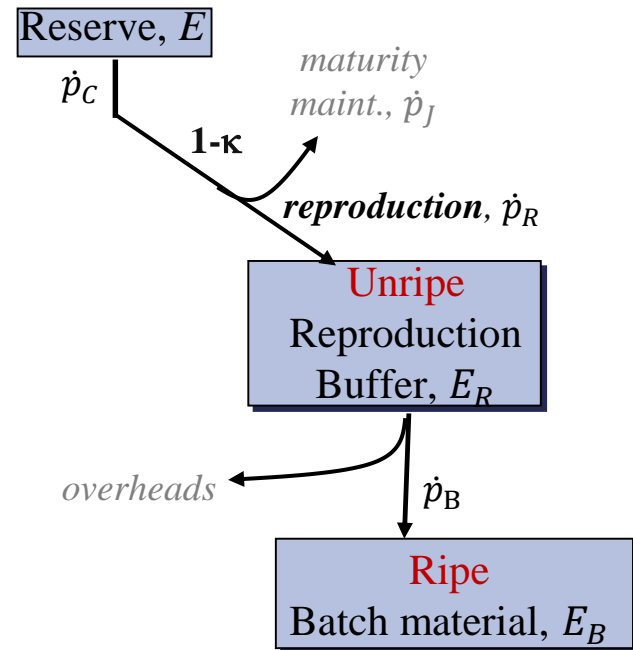
Batch initiation: e.g. $T > T_{threshold}$

Batch size $E_B^* = \min(E_R, [E_B]L^3)$

At spawning t_B

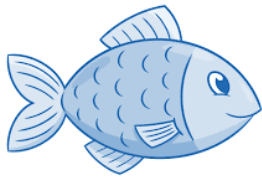
$$E_R(t_B + dt) = E_R(t_B) - E_B^*$$

$$E_B(t_B + dt) = 0$$

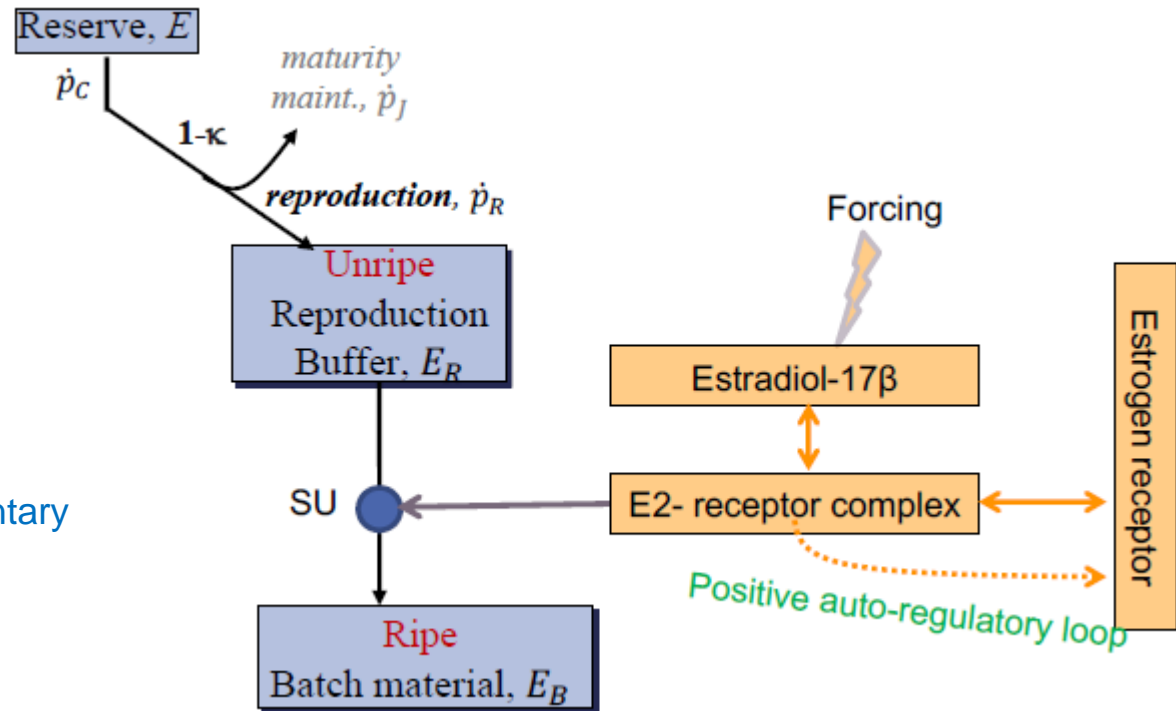


Reproduction handling rules

Link hormone dynamics underlying egg production to a DEB model

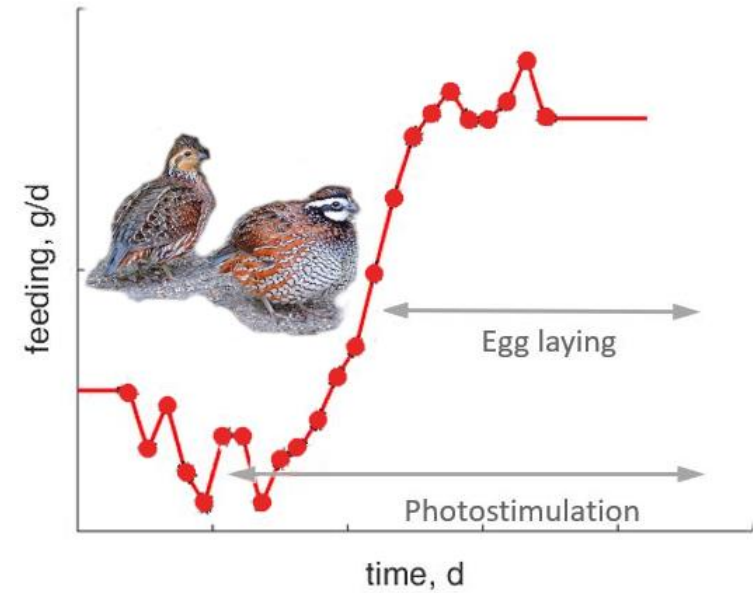
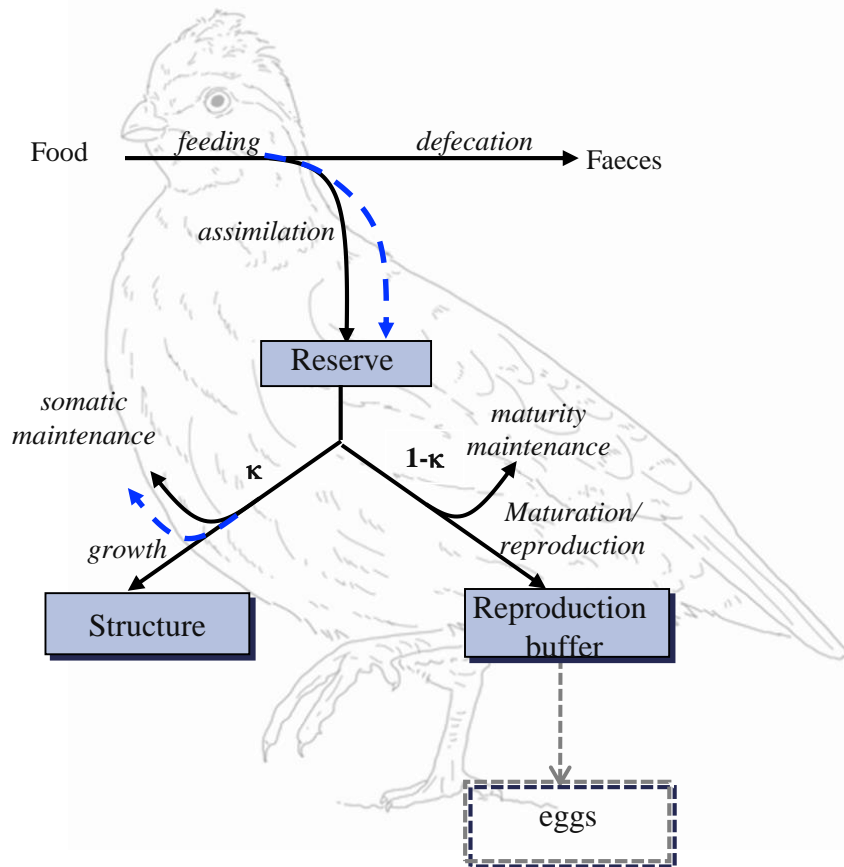


Vitellogenin synthesis:
sequential - complementary
transformation

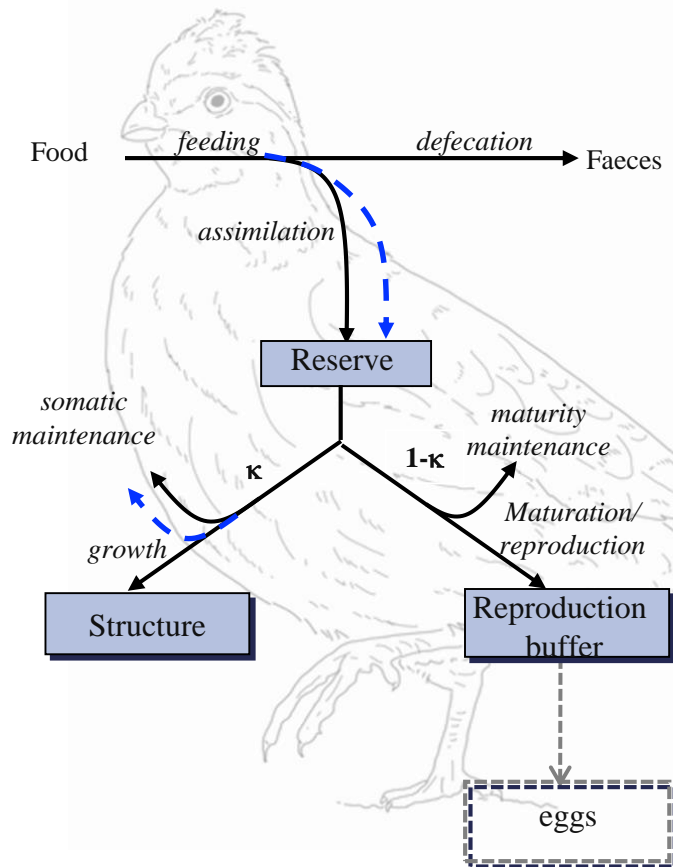


Murphy et al. (2018)
Firkus et al. (2023)

Up-regulation and reproduction



Up-regulation and reproduction



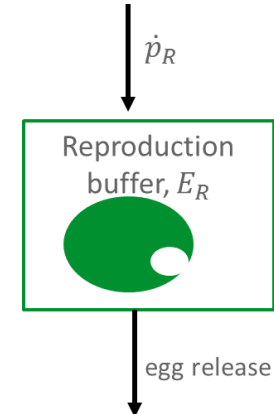
Extra assimilates are first assimilated into reserve;
up-regulation of maintenance costs

$$\dot{p}_A^R = s_x(t) \{ \dot{p}_{Am} \} f L^2 (t_0 \leq t \leq t_1)$$

$$\dot{p}_A = \dot{p}_A + \dot{p}_A^R$$

$$\dot{p}_S = (1 - s_x(t)f) [\dot{p}_M] L^3$$

Egg laying module



3. Starvation

Starvation



Rules depend on species and environmental conditions

- When mobilized reserves cannot meet **somatic maintenance** (i.e. $\kappa \dot{p}_C - \dot{p}_S < 0$), e.g.
 - A. Somatic maintenance can be paid from the (ripe or unripe) reproduction matter
 - B. Shrink in structural mass to pay the somatic maintenance
- When mobilized reserves cannot meet **maturity maintenance** (i.e. $(1 - \kappa) \dot{p}_C - \dot{p}_J < 0$)
 - Rejuvenation may occur

Starvation rules examples

A. Pay from reproduction buffer

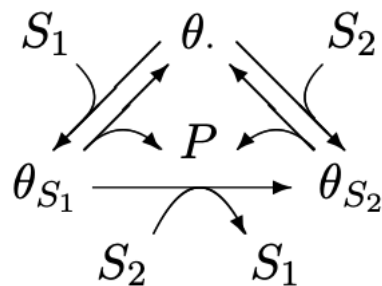
- Pecquerie et al., 2009: While ER exists, pay for p_s from ER. If the reproduction buffer is empty, the individual dies.
- Pethybridge et al., 2013; Fircus et al., 2023: pay from the reproduction buffer and/or gametes.
- Breaking down and resorption of energy from unspawned eggs.

Starvation rules

B. Shrink during starvation

Use of SUs (4.1.5 DEB3 and comments)

- The somatic maintenance-SUs receive a reserve flux and a structure flux
- Reserve and structure are **substitutable** compounds for somatic maintenance, with a strong **preference** for reserve.
- Shrinking comes with extra parameters
- Payment via structure involves an extra transformation, so extra losses.



S_1 : Structure
 S_2 : Reserve
 P : maintenance products

Figure 3.8 in DEB3

Absolute priority for reserve (4.1.5 DEB3 and comments)

- Mobilization rate

$$\dot{p}_C = E \left(\frac{\dot{v}}{L} - \dot{r} \right)$$

Growth rate

When $\frac{[E]\dot{v}}{L} > [\dot{p}_M]/\kappa$

$$\dot{r} = \frac{[E]\dot{v}/L - [\dot{p}_M]/\kappa}{[E] + [E_G]/\kappa}$$

otherwise

$$\dot{r} = \frac{[E]\dot{v}/L - [\dot{p}_M]/\kappa}{[E] + \kappa_G[E_G]/\kappa}$$

Starvation rules

Rejuvenation during starvation

When mobilized reserves cannot meet maturity maintenance (i.e. $(1 - \kappa)\dot{p}_C - \dot{p}_J < 0$)

- If the reproduction buffer is not empty, rejuvenation can be delayed by draining this buffer to supplement maturity maintenance.
- Else E_H decays exponentially (rejuvenation).

(4.1.5 comments on DEB3)

Augustine et al. (2013) Stochastic feeding in fish larvae and their metabolic handling of starvation. J of Sea Res 66 (2011) 411–418

Death by starvation

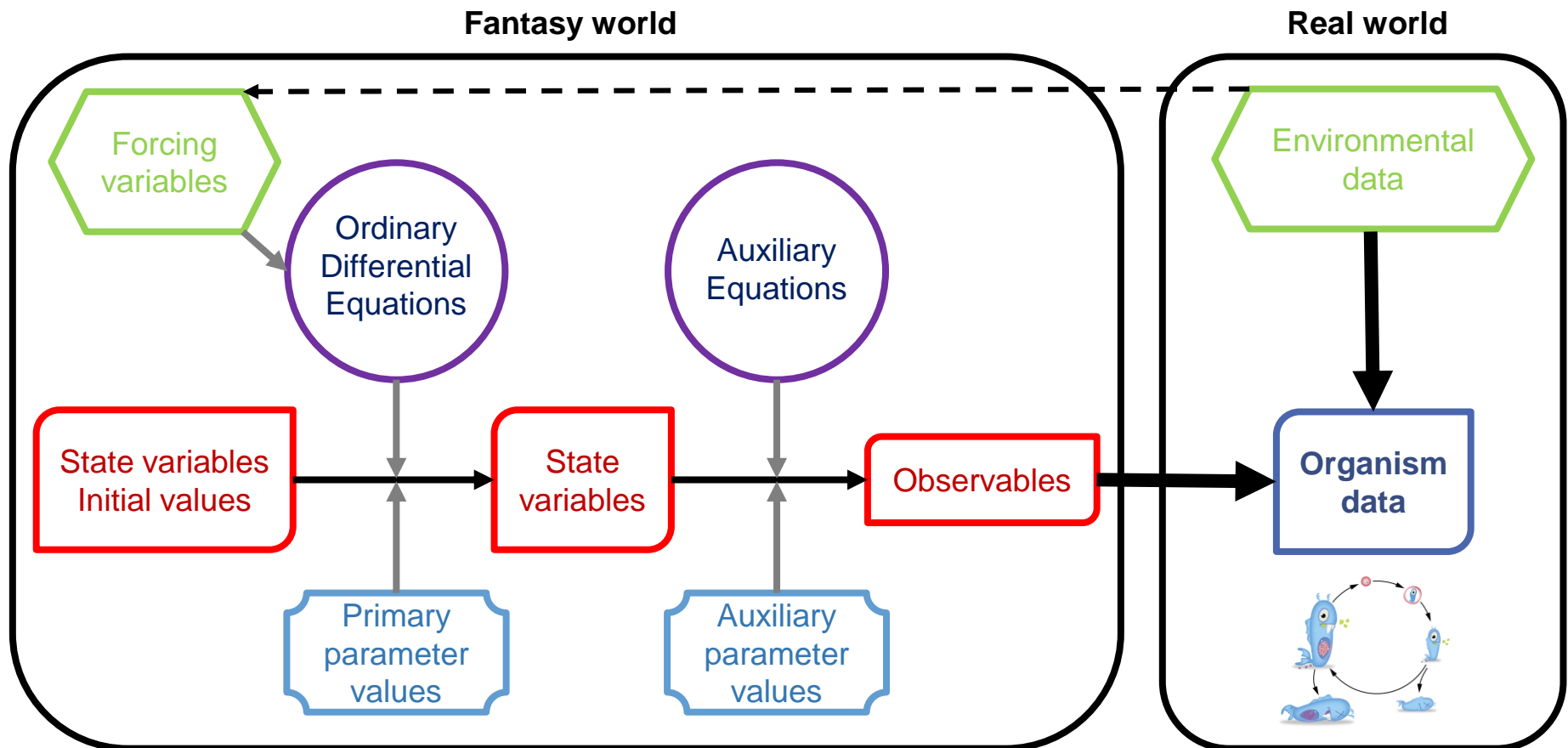


- If shrinking is allowed, death by starvation occurs if shrinking of structure exceeds a given fraction of the structure at the onset of ceasing growth.
- When the reserve is depleted to a certain extent we can assume that starvation-induced death strikes
- If the maintenance costs are being paid from the repro buffer and it is empty, the individual dies (Pecquerie et al., 2009)

4. Trajectory reconstruction

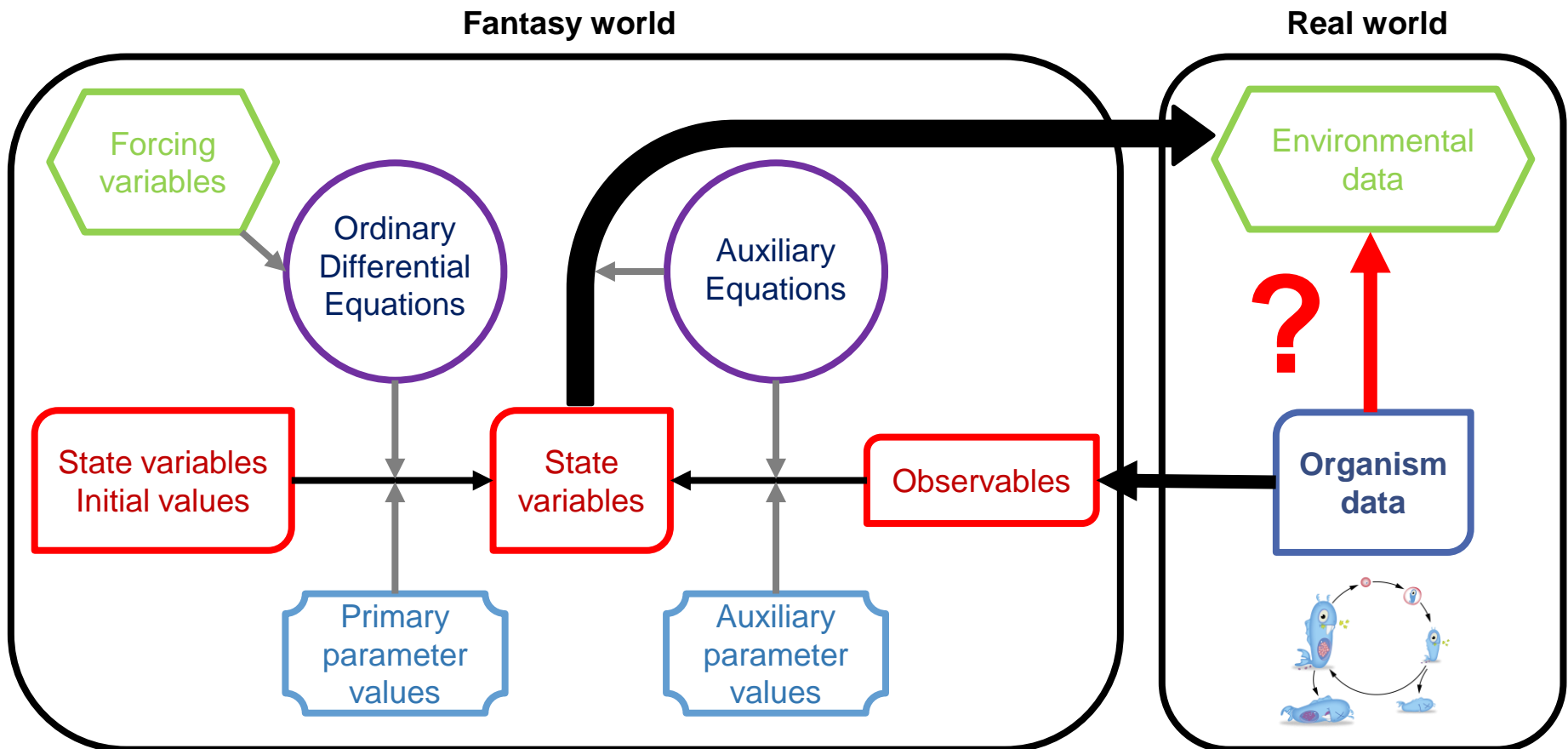
Trajectory reconstruction

Typical scheme to link real world to the model:



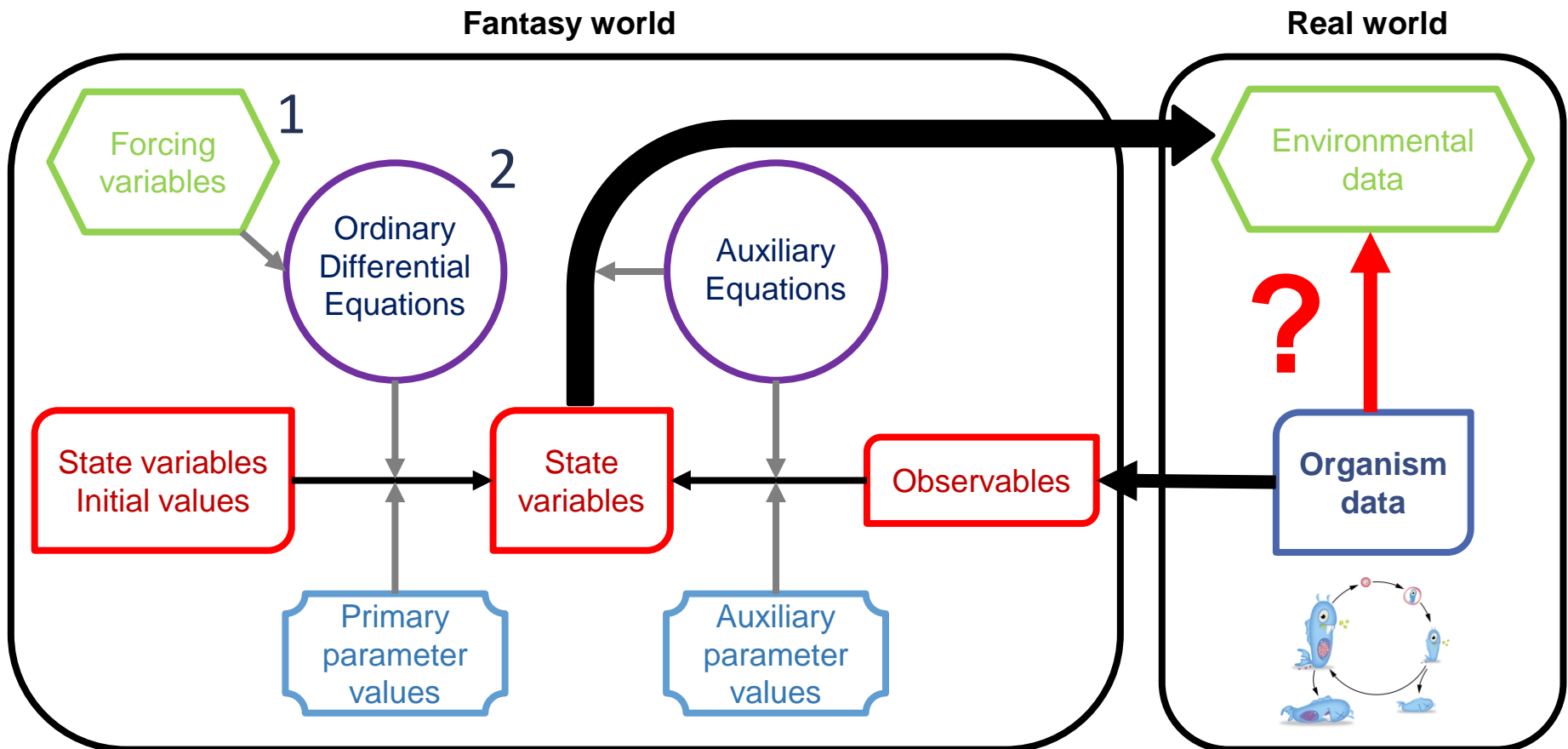
Trajectory reconstruction

Inverting the process to infer environmental data:



Trajectory reconstruction

Two methods: Fitting¹ or true inversion²



Examples of reconstruction

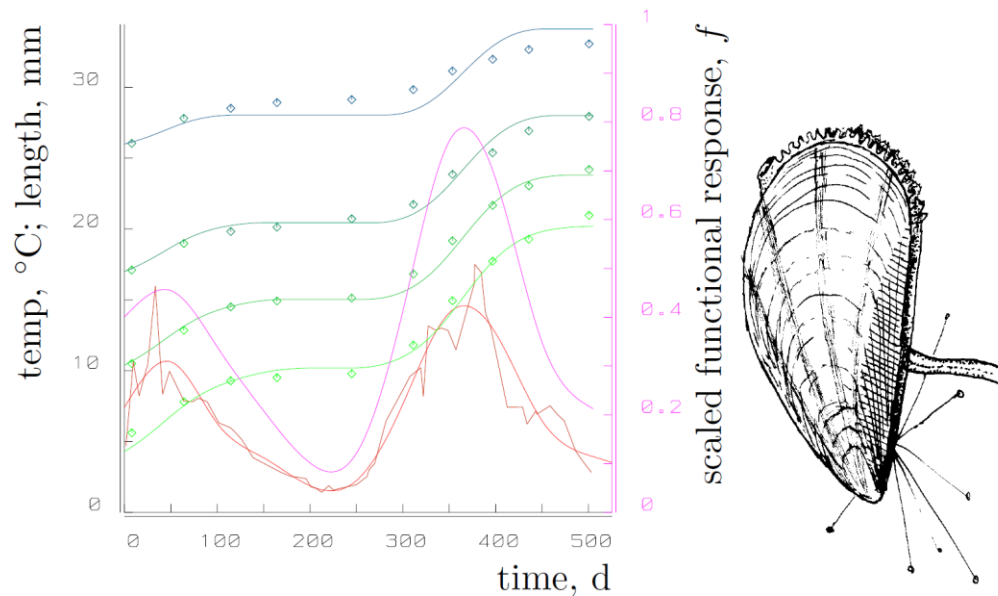
DEB3 Chapter 4.11.1



From the growth equation $\frac{dl}{dt} = \frac{f(t) - l - l_T}{f(t) + g} g k_M c_T$ we can get: $f(t) = \frac{(l - l_T) \dot{k}_M c_T}{\dot{k}_M c_T - \frac{dl}{dt} \frac{1}{g} - 1}$

Fitting a spline function through length data to get l and $\frac{dl}{dt}$

And reconstruct $f(t)$



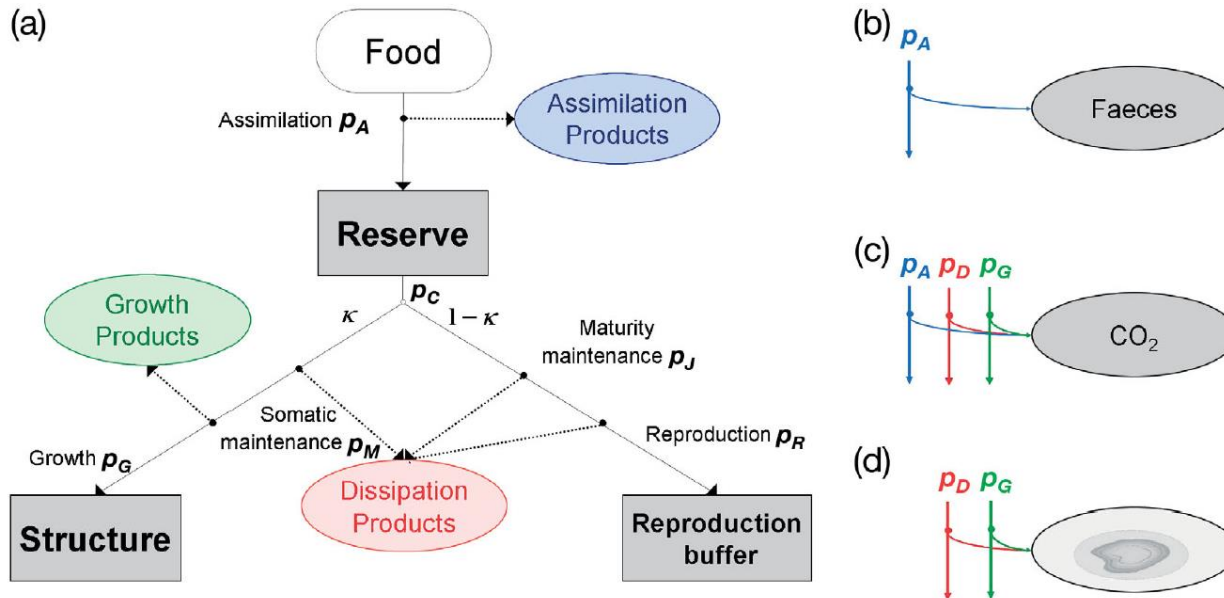
Otoliths → growth → food

Pecquerie et al. 2012

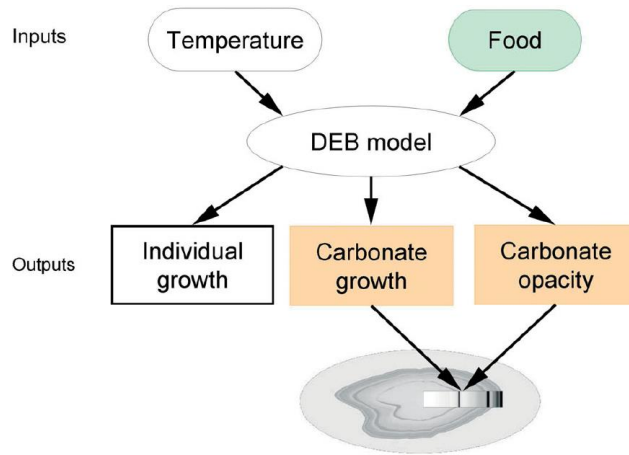


Reconstructing food conditions from biogenic carbonates (otoliths)

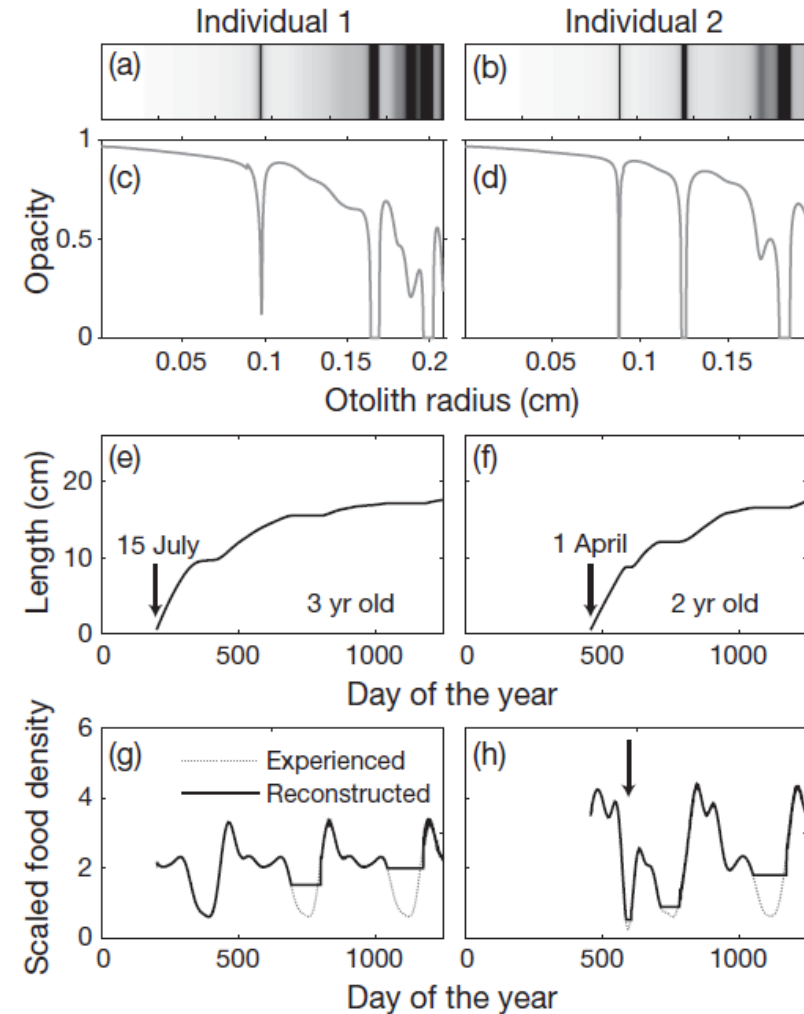
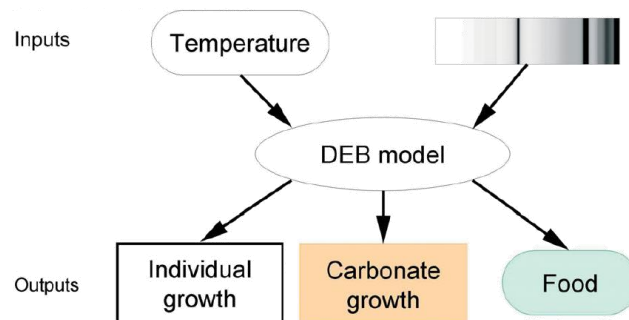
- Otoliths are DEB products, receiving contributions from growth and dissipation fluxes.
- Otolith opacity varies with food (reduced in poor conditions)



We can predict otolith growth and opacity in a normal 'forward' mode:



And use otoliths to estimate the functional response minimizing the difference between predicted and observed opacity.

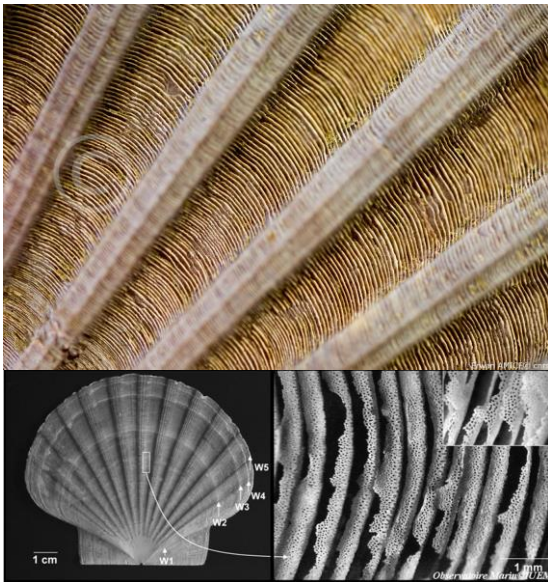


Shell growth → food & co.

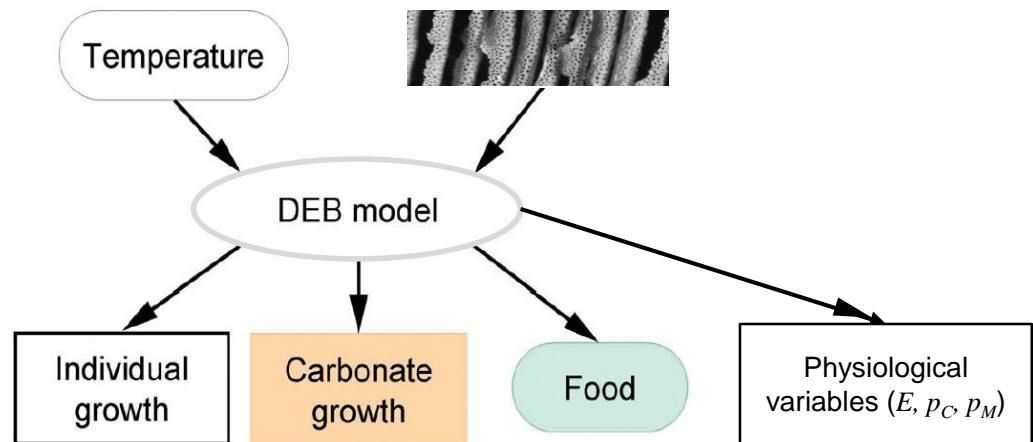
Lavaud et al. 2019

Using daily shell growth increments (and temperature to reconstruct food, reserve, reserve mobilization and maintenance.

But this time through a real inversion of the model (rewriting equations, no fitting).



Daily king scallop shell increments



The mother of formulas, essential to know, ...

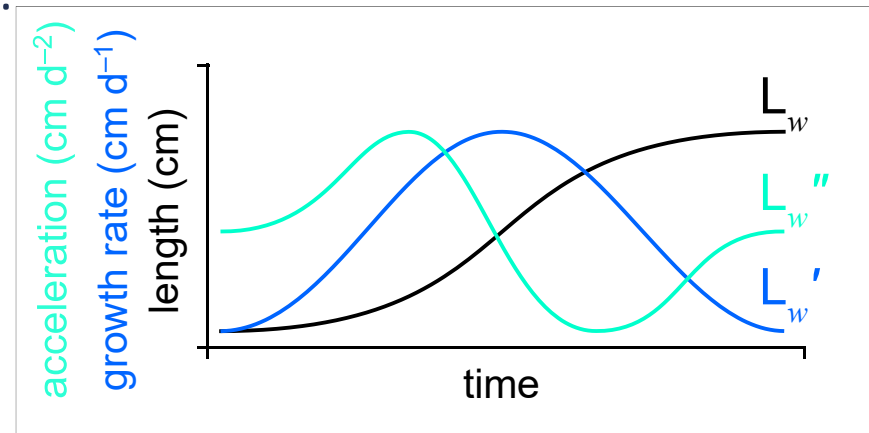
The Growth DEB equation

$$\begin{aligned}
 & -9Lg'^2 + 3LgLg'' - f\dot{v}_\delta \dot{k}_M Lg_m + 6f\dot{k}_M Lg_m Lg' + 3\dot{v}_\delta Lg' \\
 & + \dot{v}_\delta \dot{k}_M Lg - 2\dot{k}_M Lg Lg' - 9f \frac{\dot{k}_M Lg_m}{\dot{v}_\delta} Lg'^2 - 3 \frac{\dot{k}_M}{\dot{v}_\delta} Lg Lg'^2 + 3 \frac{\dot{k}_M}{\dot{v}_\delta} Lg^2 Lg'' \\
 & - 3 \left(1 + \frac{\dot{k}_M}{\dot{v}_\delta} Lg \right) Lg Lg' \frac{T_A T'}{T^2} = 0
 \end{aligned}$$

where $\dot{v}_\delta = \frac{\dot{v}}{\delta}$, $\dot{k}_M = \frac{[\dot{p}_M]}{[E_G]}$ and $Lg_m = \frac{L_m}{\delta}$, T_A is the Arrhenius temperature.

Actually, just a linear rewriting of the DEB differential equations, using:

- 1 variable, L_w
- 5 parameters \dot{k}_M , L_m , \dot{v} , δ_M , and T_A .

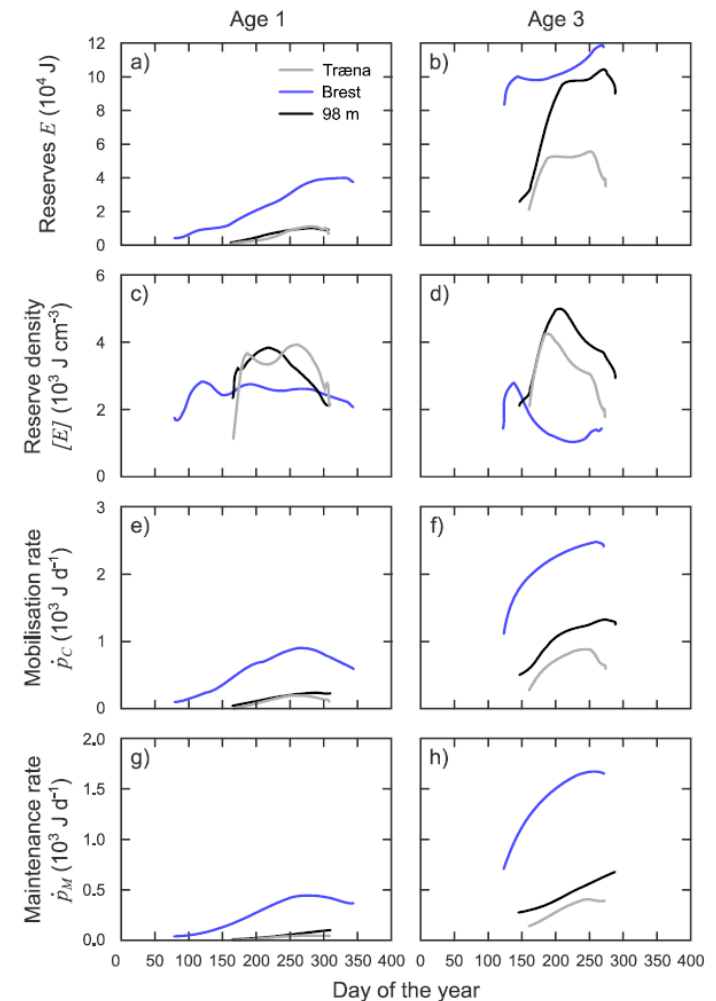
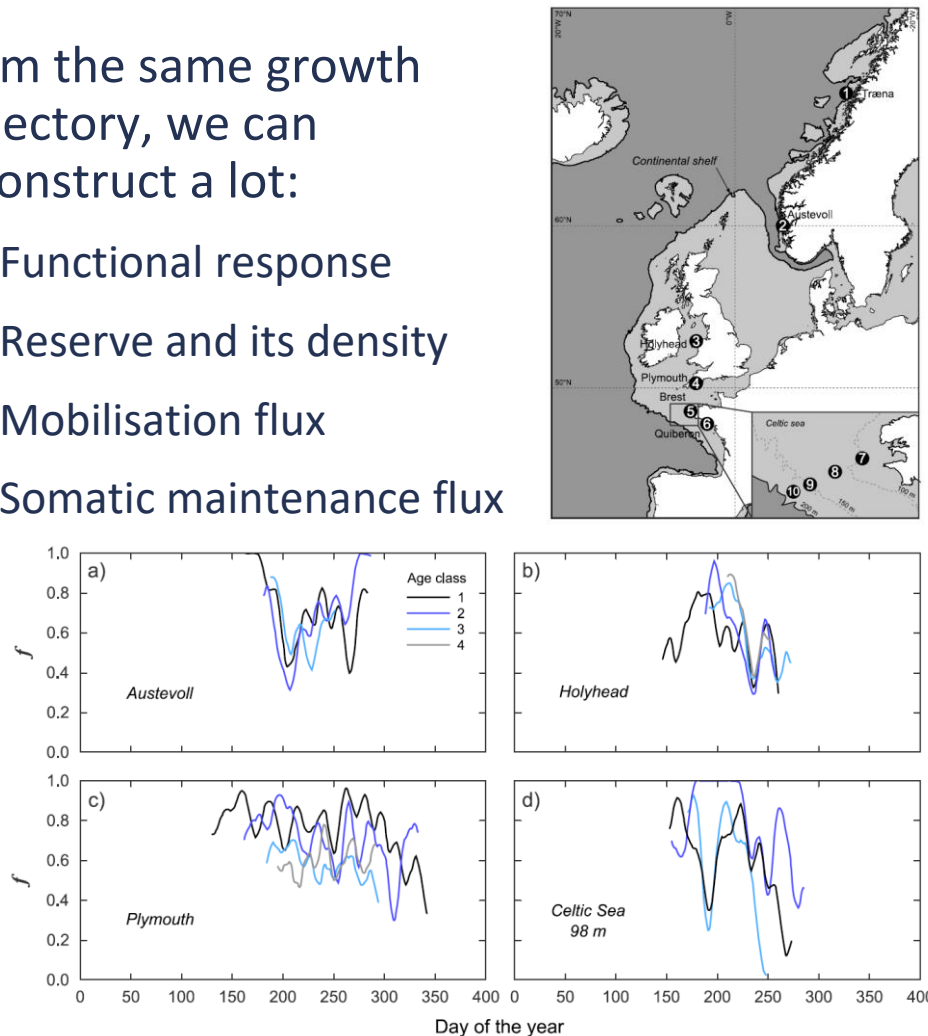


Examples of reconstruction

Lavaud et al. 2019

From the same growth trajectory, we can reconstruct a lot:

- Functional response
- Reserve and its density
- Mobilisation flux
- Somatic maintenance flux



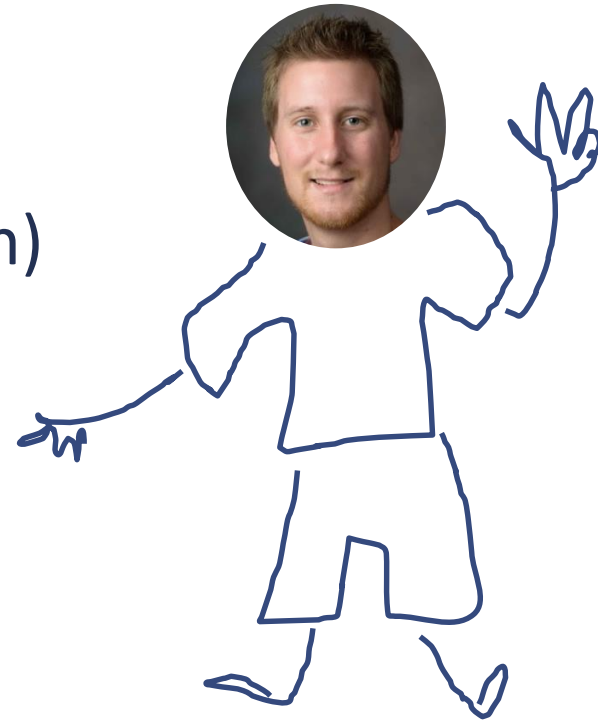
Thank you!

Questions?

Nina, Dina, Orestis, (Romain)

* Slides will be online! ;)

nmarn@irb.hr



rlavaud@agcenter.lsu.edu