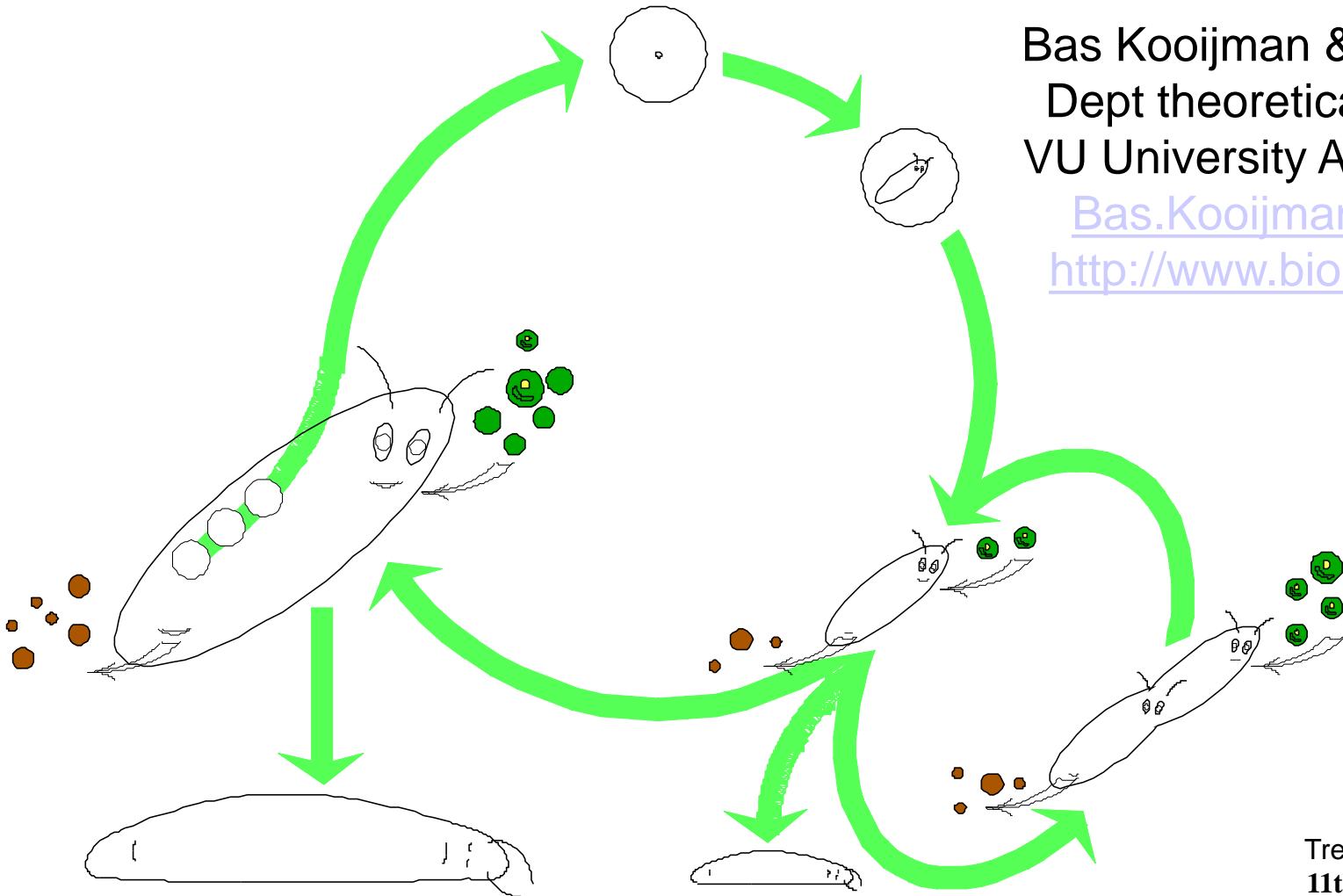


40 yrs of development and application of DEB theory

Bas Kooijman & Bob Kooi
Dept theoretical biology
VU University Amsterdam

Bas.Kooijman@vu.nl
<http://www.bio.vu.nl/thb>



Trento, 2020/02/04
11th DSABNS 2020

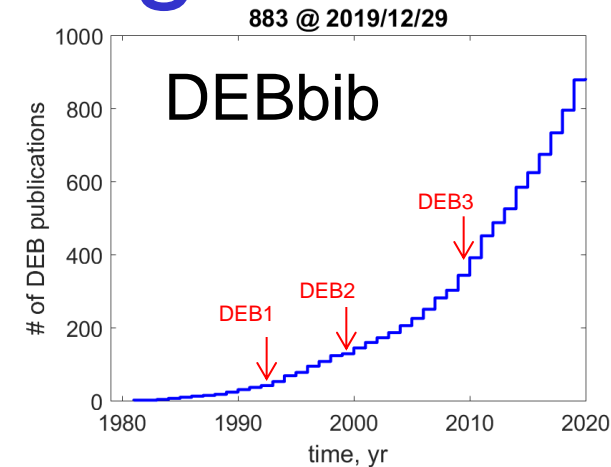
Dynamic Energy Budget

Start: Aug 1979 understanding effects of toxicants

Now: bibliography of 883 DEB papers:

https://www.zotero.org/groups/500643/deb_library/

@2020: 2 DEB papers appear per week



Dynamic:

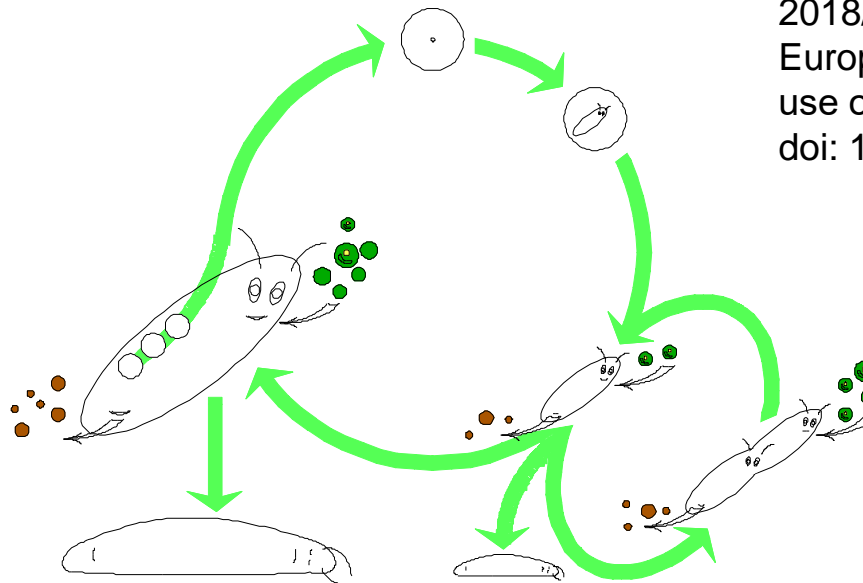
- Full life cycle (embryo, juvenile, adult) in changing environment (temp, food)

Energy:

- Feeding
- Digestion
- Storing
- Growth
- Maturation
- Maintenance
- Reproduction
- Product formation
- Aging

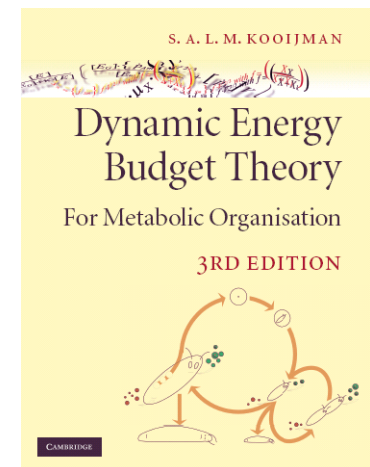
Budget:

- Conservation: energy, mass, time, isotopes



2018/06/27

European Food Safety Authority:
use of DEB's for risk assessment
doi: 10.2903/j.efsa.2018.5377



Homeostasis

strong homeostasis

constant composition of pools (reserves/structures): mass conservation!
generalized compounds, stoichiometric constraints on synthesis
respiration/heat follows from closing balances for chemical elements

weak homeostasis

constant composition of biomass during growth in constant environments
presumes strong homeostasis and determines reserve dynamics

structural homeostasis

constant relative proportions during growth in constant environments
isomorphy: surface \propto length², volume \propto length³

thermal homeostasis

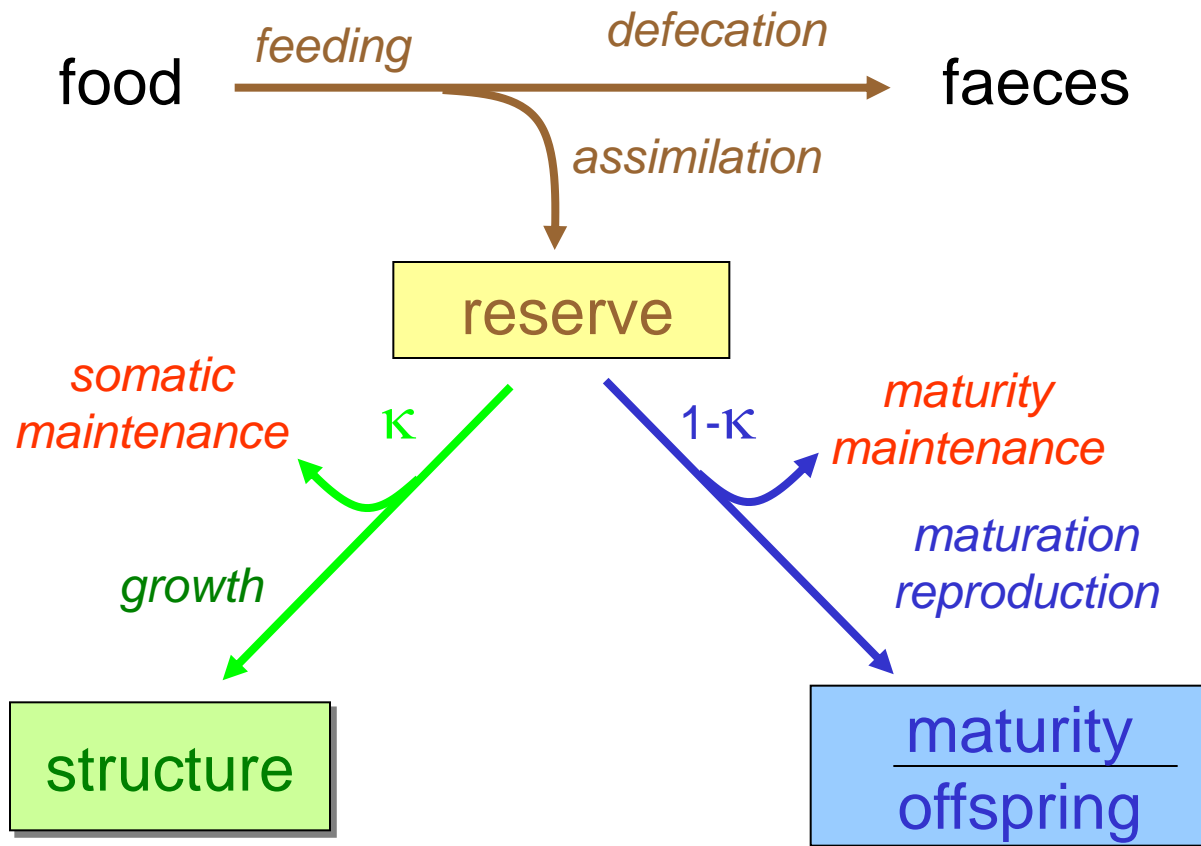
ectothermy \rightarrow homeothermy \rightarrow endothermy

acquisition homeostasis

supply \rightarrow demand systems

Standard DEB scheme

1 food type, 1 reserve, 1 structure, isomorph



time: searching & handling
 feeding \propto surface area
 weak & strong homeostasis
 k-rule for allocation to soma
 maintenance has priority
 somatic maint \propto structure
 maturity maint \propto maturity
 stage transition: maturation
 embryo: no feeding, reprod
 juvenile: no reproduction
 adult: no maturation
 maternal effect: reserve density
 at birth equals that of mother
 initially: zero structure, maturity
 egg = blob of reserve
 reproduction
 via reproduction buffer
 buffer handling rules

Empirical special cases of DEB

year	author	model	year	author	model
1780	Lavoisier	multiple regression of heat against mineral fluxes	1950	Emerson	cube root growth of bacterial colonies
1825	Gompertz	Survival probability for aging	1951	Huggett & Widdas	foetal growth
1889	Arrhenius	temperature dependence of physiological rates	1951	Weibull	survival probability for aging
1891	Huxley	allometric growth of body parts	1955	Best	diffusion limitation of uptake
1902	Henri	Michaelis--Menten kinetics	1957	Smith	embryonic respiration
1905	Blackman	bilinear functional response	1959	Leudeking & Piret	microbial product formation
1910	Hill	Cooperative binding	1959	Holling	hyperbolic functional response
1920	Pütter	von Bertalanffy growth of individuals	1962	Marr & Pirt	maintenance in yields of biomass
1927	Pearl	logistic population growth	1973	Droop	reserve (cell quota) dynamics
1928	Fisher & Tippitt	Weibull aging	1974	Rahn & Ar	water loss in bird eggs
1932	Kleiber	respiration scales with body weight ^{3/4}	1975	Hungate	digestion
1932	Mayneord	cube root growth of tumours	1977	Beer & Anderson	development of salmonid embryos

DEB theory is axiomatic,
based on mechanisms

not meant to glue empirical models

Since many empirical models

turn out to be special cases of DEB theory

the data behind these models support DEB theory

This makes DEB theory very well tested against data

Inter-species body size scaling

- parameter values tend to co-vary across species
- parameters are either intensive or extensive
- appropriate ratios of extensive parameters are intensive
- maximum structural length is $L_m = \frac{\kappa\{p_{Am}\}}{[p_M]}$
 - κ allocation fraction to soma (intensive)
 - $[p_M]$ volume-specific som maintenance power (intensive)
 - $\{p_{Am}\}$ surface area-specific assimilation power (extensive)
- conclusion: $\{p_{Am}\} \propto L_m$
- write physiological property as function of parameters (including maximum body weight)
- evaluate this property as function of max body weight

Add_my_Pet (AmP)

- www.bio.vu.nl/thb/deb/deblab/add_my_pet/
- referenced data, par-estimates, implied properties, Matlab code
- par-point-estimation: minimization of new loss function
- par-interval-estimation: calibrated loss function profile
- Although DEB applies to all organisms,
AmP only for animals because they feed on other organisms

Board of curators [\(click here for history\)](#)



Bas Kooijman
(Managing curator)
VU Univ. A'dam



Dina Lika
University
of Crete



Starrlight Augustine
Akvaplan-niva
AS, Tromsø



Michael Kearney
R-issues, NicheMapR
Melbourne Univ.

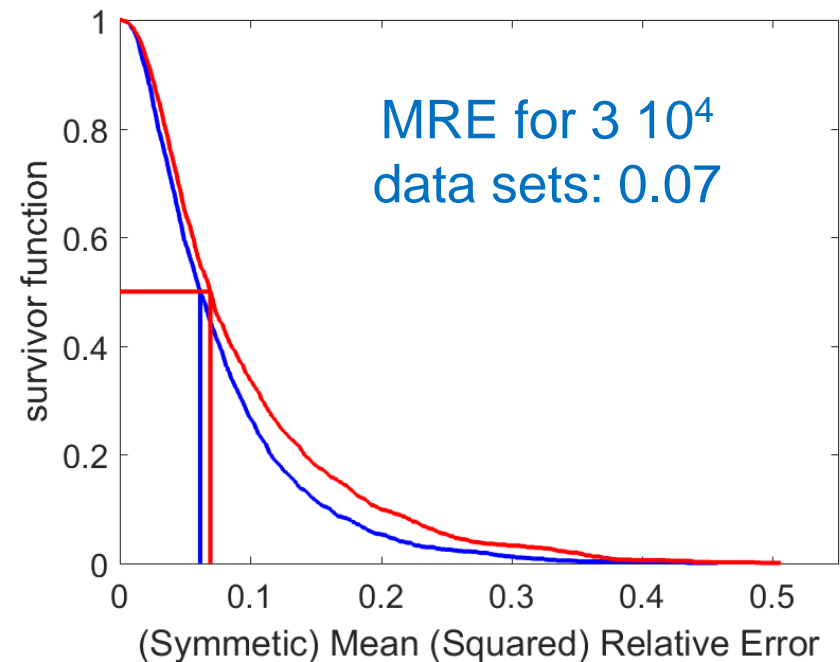
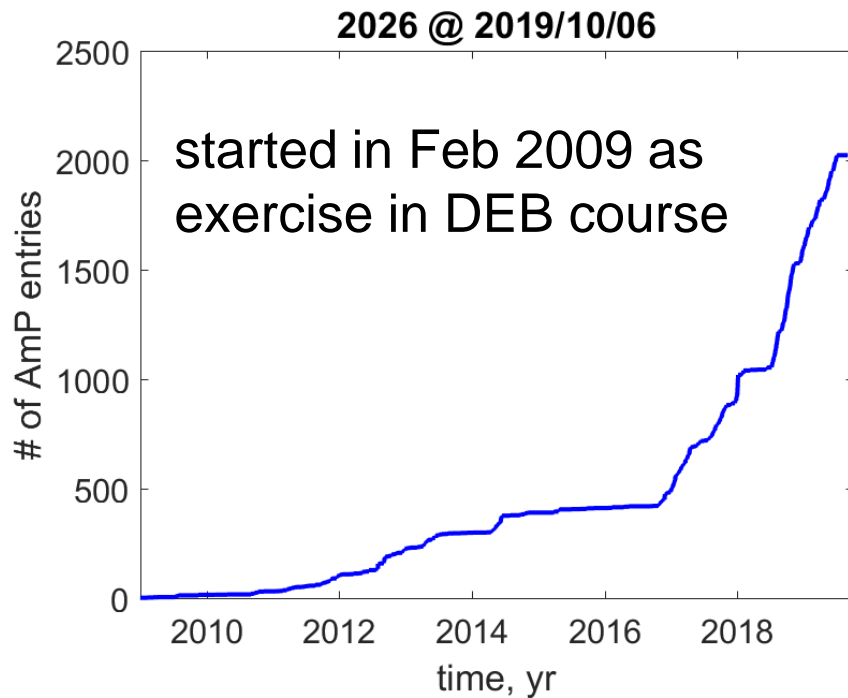


Nina Marn
Communication
Zagreb Univ.

Marques et al (2018) The AmP project, *PLoS Comp Biol* . **14**(5): e1006100

Marques et al (2019) Fitting multiple models to multiple data. *J. Sea Res.* **143**: 48-56

AmP entries & fit



$$\text{MRE} = \sum_{i=1}^n \sum_{j=1}^{n_i} \frac{w_{ij}}{nw_i} \frac{|p_{ij} - d_{ij}|}{|d_i|}$$

$$\text{SMSE} = \sum_{i=1}^n \sum_{j=1}^{n_i} \frac{w_{ij}}{nw_i} \frac{(p_{ij} - d_{ij})^2}{d_i^2 + p_i^2}$$

$$d_i = \sum_{j=1}^{n_i} \frac{d_{ij}}{n_i}; p_i = \sum_{j=1}^{n_i} \frac{p_{ij}}{n_i}; w_i = \sum_{j=1}^{n_i} \frac{w_{ij}}{n_i}$$

Metabolic acceleration

Def: long-term increase of respiration
relative to standard DEB expectation

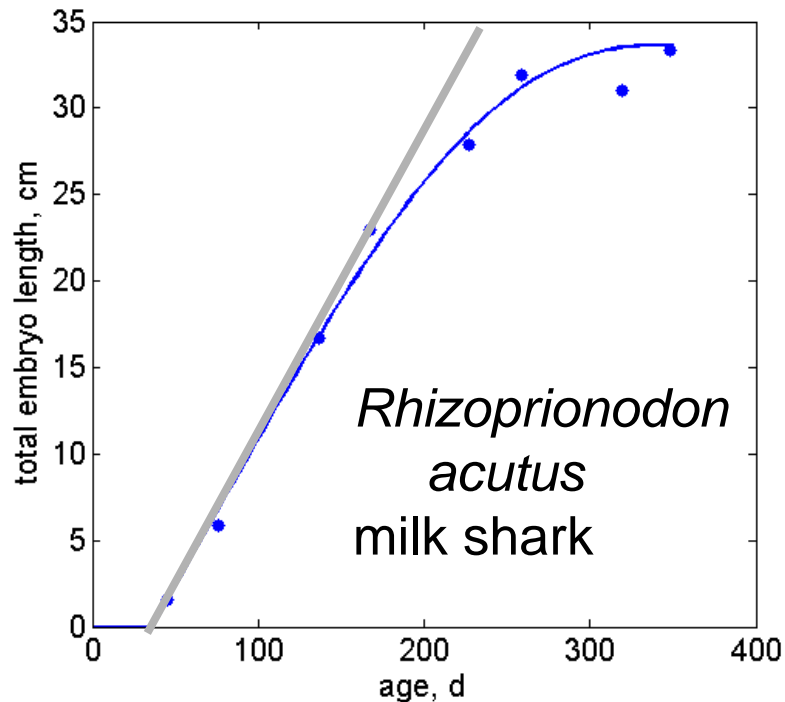
Types of acceleration

- R: maturation
- X: food (diet)
- A: assimilation
- M: morph
- T: temperature

Short-term increase in respiration (no metabolic acceleration)

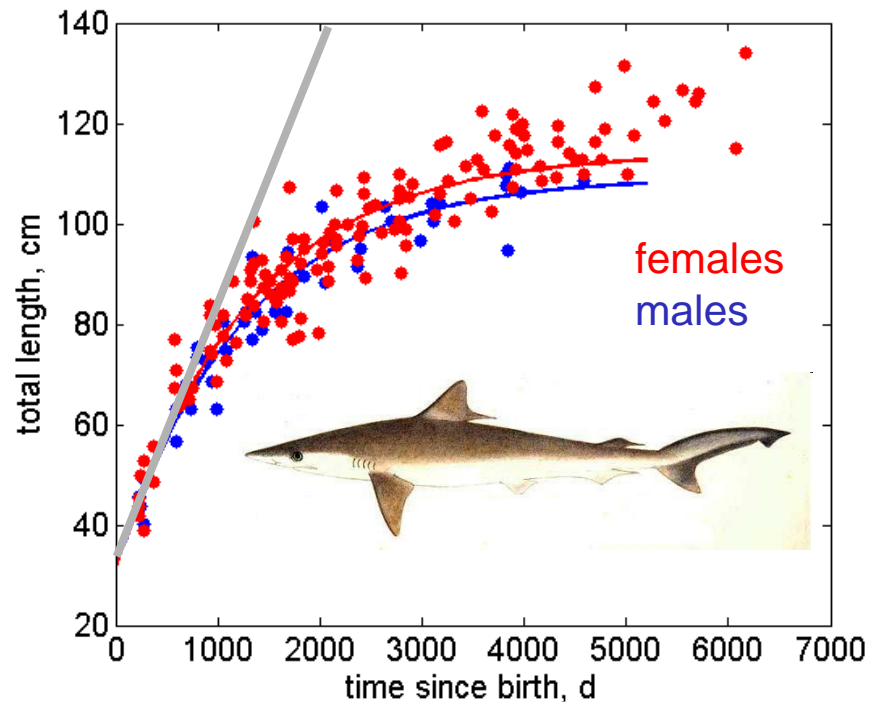
- heat increment of feeding
- boosts of activity
- migration
- pregnancy/ lactation

Standard DEB model: growth



$$\frac{d}{dt}L(0) = \frac{\dot{v}}{3}$$

t	time
L	structural length
a_b	age at birth
l_b	scaled length at birth
\dot{v}	energy conductance
e	scaled reserve density
g	energy investment ratio



$$\frac{d}{dt}L(a_b) = \frac{\dot{v}}{3} \frac{e - l_b}{e + g}$$

Type M acceleration

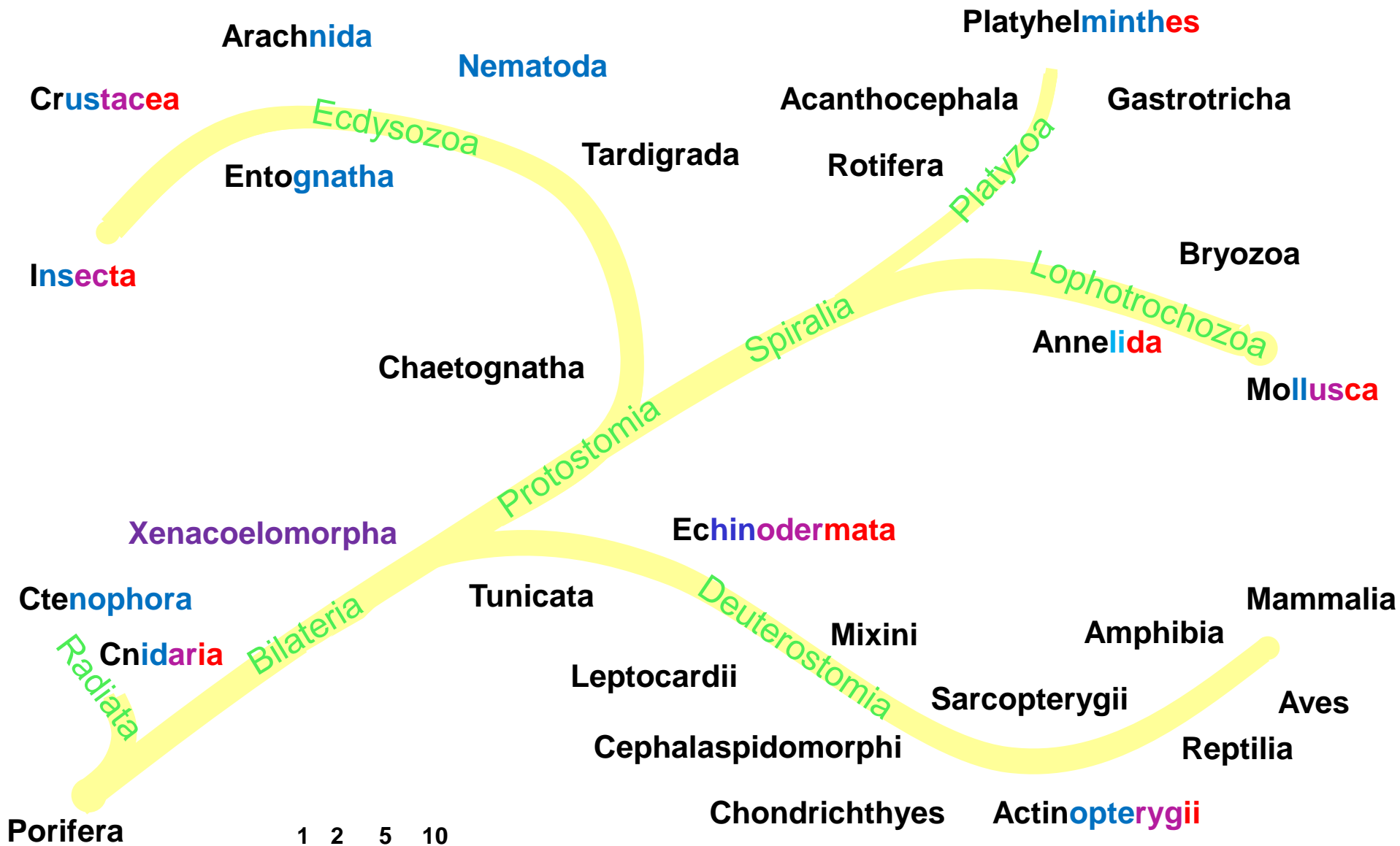
Def: increase of potential food intake during ontogeny,
combined with increase in potential mobilisation

Increase of specific assimilation $\{p_{Am}\}$ and energy conductance v
with length from birth to metamorphosis

No change in reserve capacity

One-parameter extension of standard DEB model:
maturity level at metamorphosis

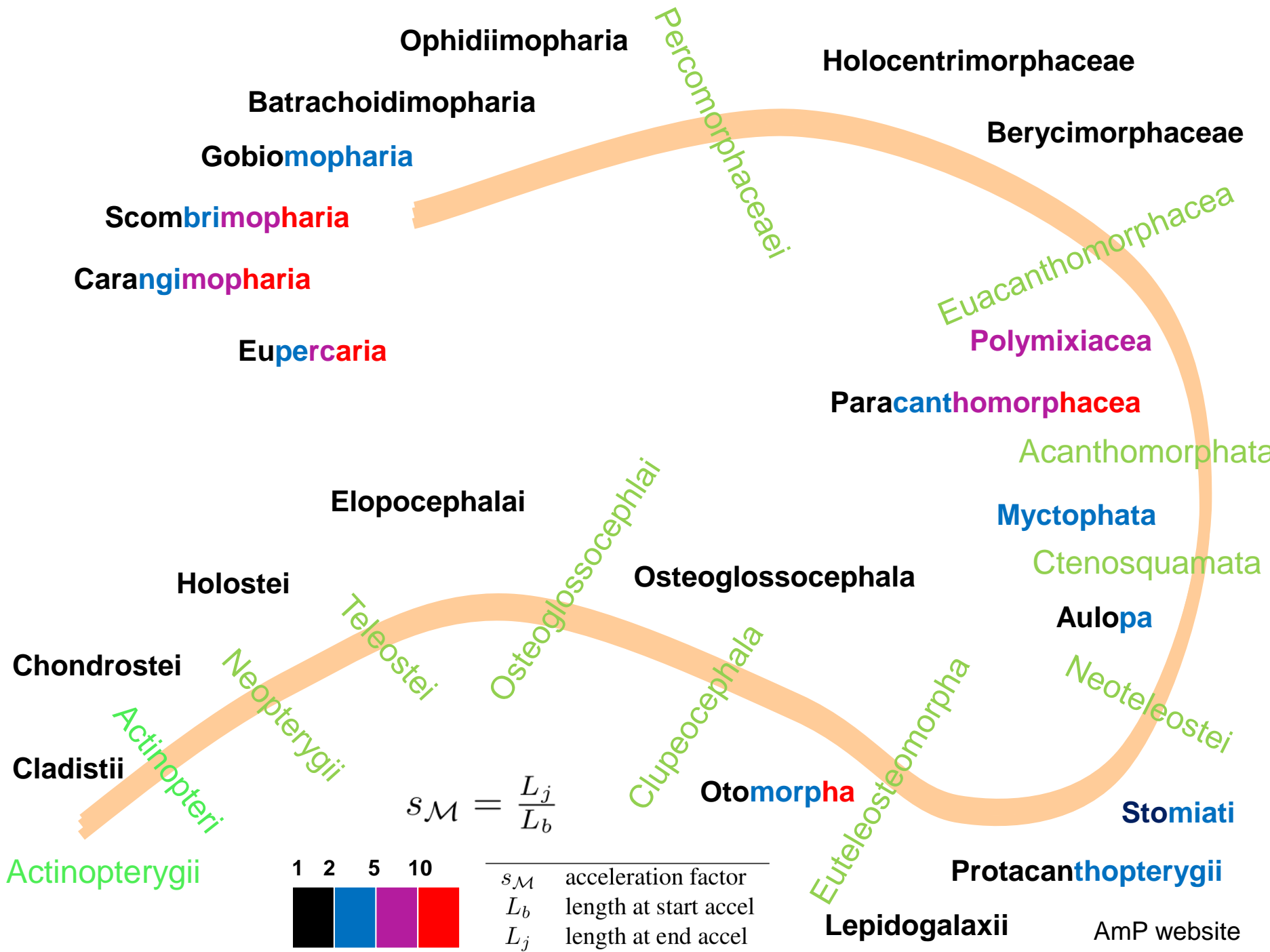
Frequently linked to larval stages,
but e.g. amphibians don't accelerate



$$s_{\mathcal{M}} = \frac{L_j}{L_b}$$

1	2	5	10
Black	Blue	Purple	Red

$s_{\mathcal{M}}$	acceleration factor
L_b	length at start accel
L_j	length at end accel



Supply-demand spectrum

Supply

eat what is available

high half saturation coefficient
can handle large range of intake
reserve density varies wildly
large range of ultimate sizes
survives some shrinking well
physiological birth control
low peak metabolic rate
open circulatory system
iso- & centro-lecithal eggs
rather passive, simple behaviour
sensors less developed
typically ectothermic
evolutionary original
has demand components
(maintenance)

metabolic control external

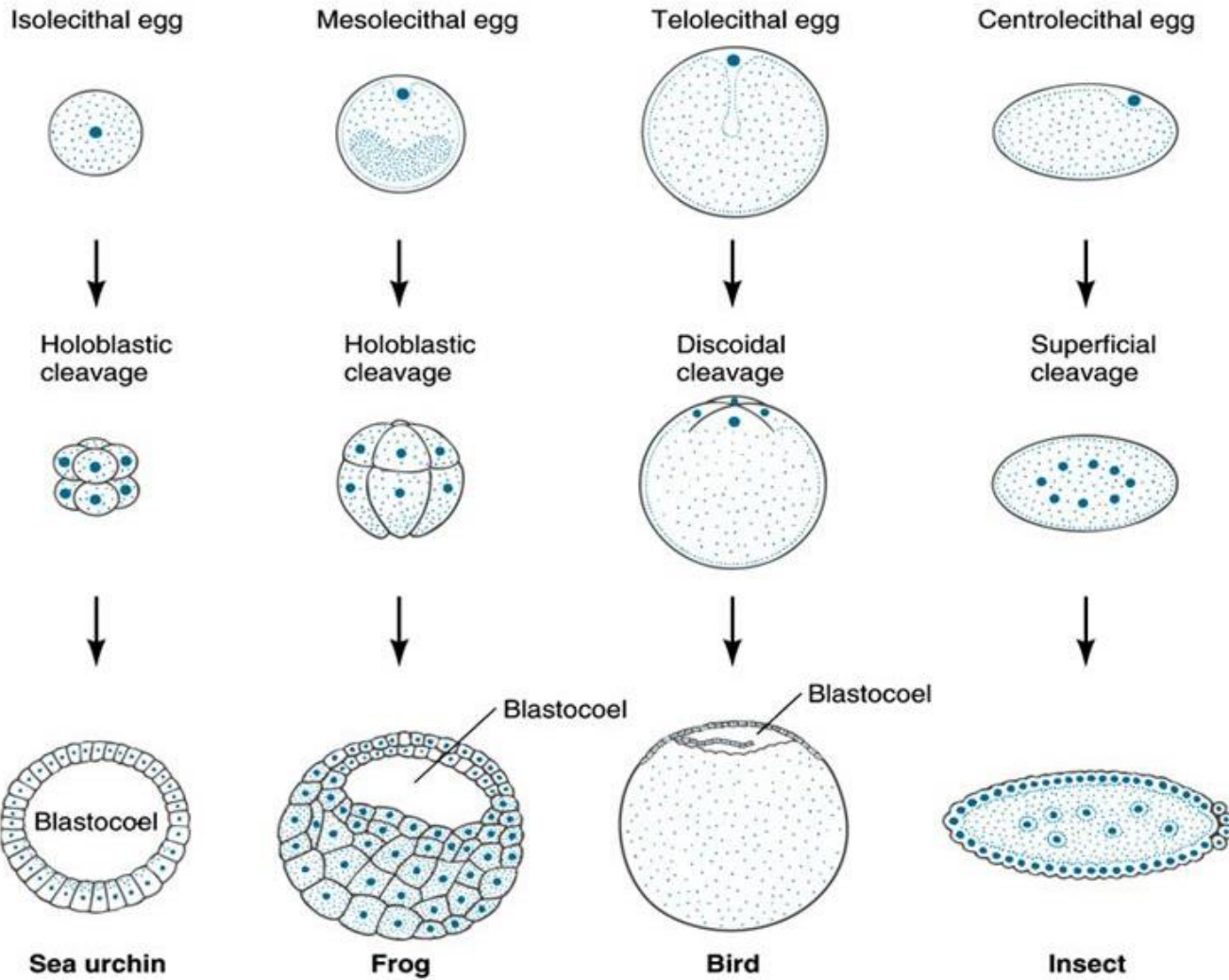
Demand

eat what is needed

low half saturation coefficient
can handle small range of intake
reserve density varies little
small range of ultimate sizes
survives shrinking badly
behavioural birth control
high peak metabolic rate
closed circulatory system
a- & telo-lecithal eggs
rather active, complex behaviour
sensors well developed
typically endothermic
evolved from supply systems
has supply components
(some food must be available)

metabolic control internal

Embryo development



supply, slow
no capillaries

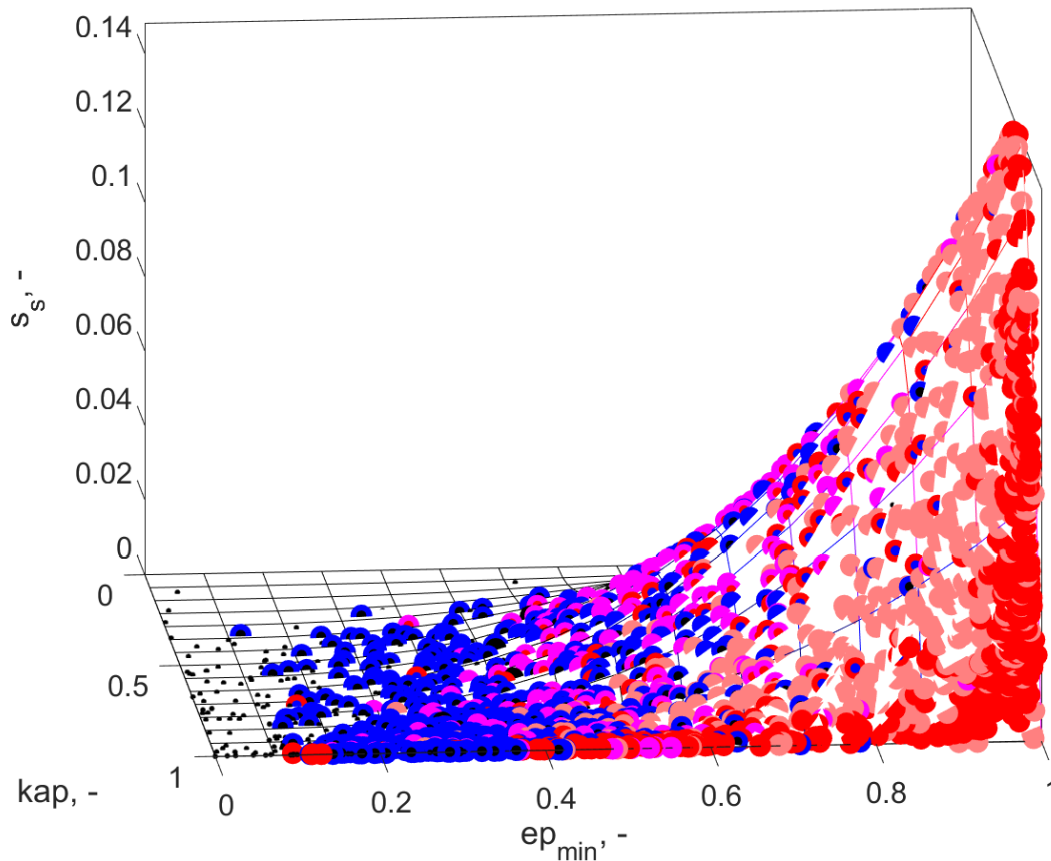
demand, fast
capillaries

Supply-demand spectrum

AmPtool/mydata_shstat
example 4, n = 2026

$$s_s = \frac{\dot{p}_J \dot{p}_M^2}{\dot{p}_A^3} = \frac{\dot{p}_J}{\dot{p}_A} \kappa^2$$

s_s	supply stress
\dot{p}_J	maturity maintenance
\dot{p}_M	somatic maintenance
\dot{p}_A	assimilation
κ	allocation fraction to soma
e_p^{\min}	scaled func resp such that growth ceases at puberty



- Cyclostomata
- Chondrichthyes
- Actinopterygii
- Latimeria
- Dipnoi
- Amphibia
- Lepidosauria
- Aves
- Archelosauria
- Mammalia
- Animalia

The small deviations from the surface $s_s(\kappa, e_p^{\min}) = e_p^3 \kappa^2 (1-\kappa)$ are caused by acceleration s_M depending on food level

Extremes in relative maturity at birth in fish

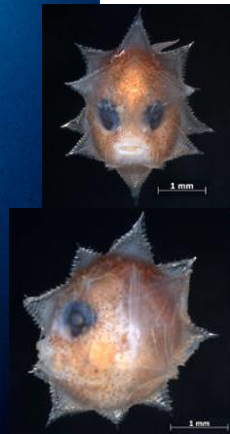
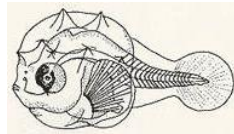
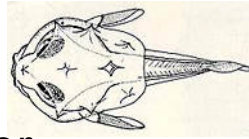
Mola mola (**ocean sunfish**)

♂, ♀ 4 m, 1500 (till 2300) kg

Egg: 1.3 mg, 3×10^{10} eggs in buffer

At birth: 1.84 mm g; $a_b = 0.6$ d

Feeds on jellyfish & combjellies



Latimeria chalumnae (**coelacanth**)

♂, ♀ 1.9 m, 90 kg

Egg: 325 g, 15 eggs in buffer

At birth: 30 cm; $a_b = 395$ d

Feeds on fish

Population growth

Characteristic equation

$$1 = \int_0^{\infty} S(a) \dot{R}(a) \exp(-\dot{r}_N a) da \quad \dot{r}_N = \dot{R}_m \text{ for } S(a) = 1 \text{ \& } \dot{R}(a) = \dot{R}_m$$

Ceiling of spec pop growth rate

$$\exp(-\dot{r}_N^m a_p) = \dot{r}_N^m / \dot{R}_m \quad \text{for } S(a) = 1; \quad \dot{R}(a) = (a > a_p) \dot{R}_m$$

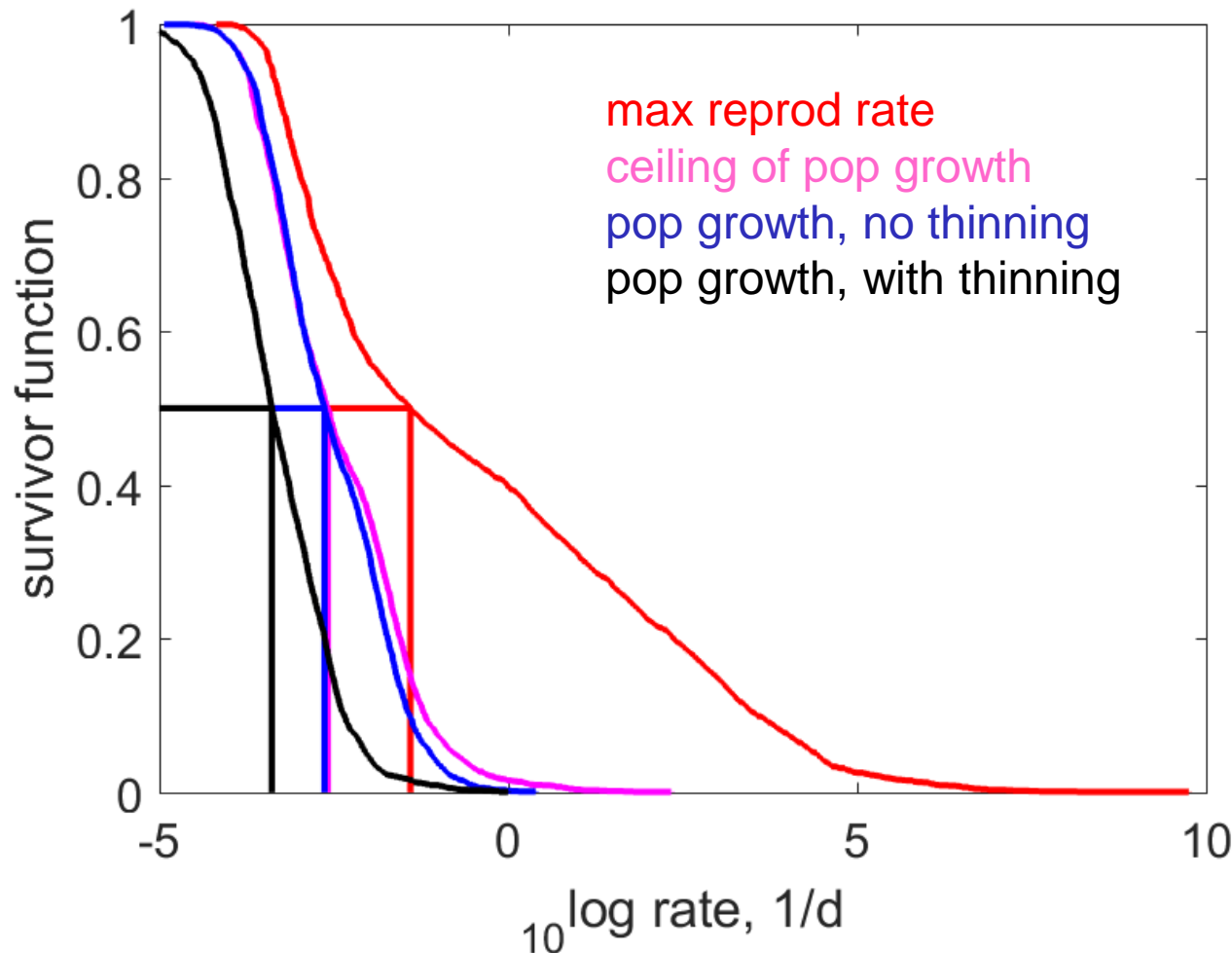
Thinning

$$\dot{J}_X^N(a) = N_0 S(a) \{\dot{J}_X\} L^2(a); \quad \frac{d}{da} \dot{J}_X^N = 0 \quad \rightarrow \quad \dot{h}(a) = \dot{r}(a) \frac{2}{3}$$

a	age	a_p	age at puberty
S	survival prob	\dot{h}	hazard rate: $-\frac{d}{da} \ln S$
L	(structural) length	\dot{J}_X^N	feeding rate of cohort
\dot{R}	reprod rate	$\{\dot{J}_X\}$	spec feeding rate: \dot{J}_X / L^2
\dot{r}	spec body growth rate: $\frac{d}{da} \ln L^3$	\dot{r}_N	spec pop growth rate
N_0	# individuals in cohort at 0		

Reproduction vs pop growth

2026 AmP entries, abundant food, 20°C



What dominates pop growth?

max reprod rate

age at pub

surv prob at early age

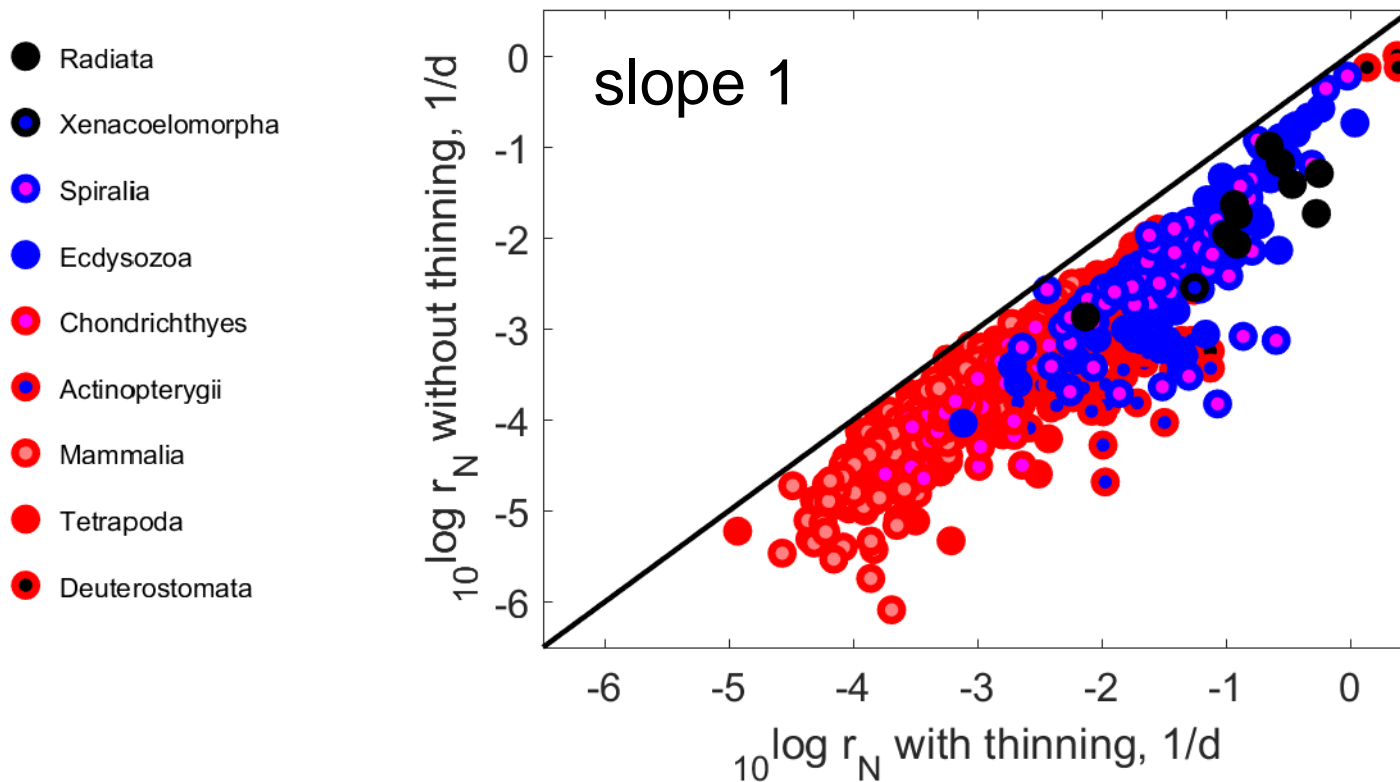
What is less important?

age-dependent reprod

aging

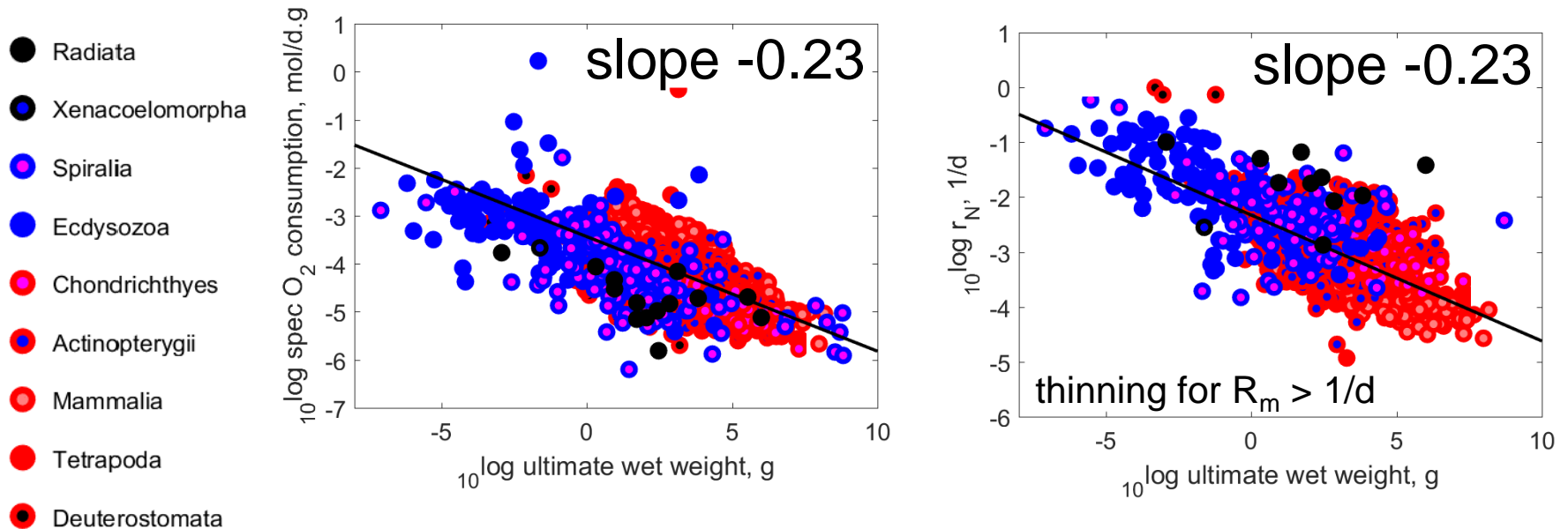
Effect of thinning

2026 AmP entries, abundant food, 20°C



Pop growth scales as respiration

2026 AmP entries, abundant food, 20°C

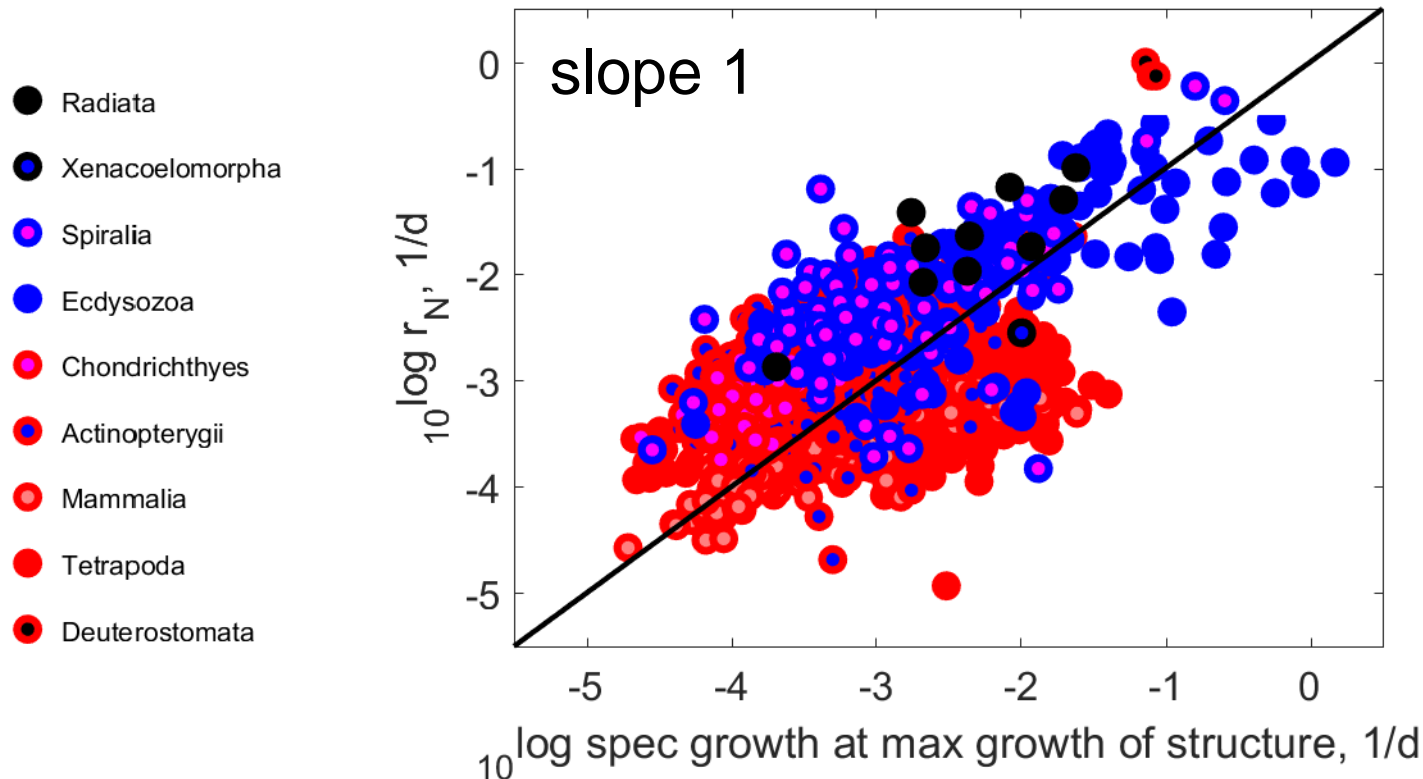


explanation:

respiration because reserve density increases (no resp for reserve)
pop growth because a_p increases and R_m decreases
(reproduction hardly contributes to respiration)

Pop growth \cong spec growth at max

2026 AmP entries, abundant food, 20°C



thinning for $R_m > 1/d$

spec growth at max growth = $\frac{3}{2}$ von Bertalanffy growth

for dividing organisms: pop growth = spec growth!

40 yrs of development and application of DEB theory

**Organisation DSABNS 2020 :
Thank you for inviting**

Bas Kooijman & Bob Kooi
Dept theoretical biology
VU University Amsterdam

Bas.Kooijman@vu.nl
<http://www.bio.vu.nl/thb>

**Audience:
Thank you for your attention
Questions are welcome**

**Slides available at
<https://www.bio.vu.nl/thb/users/bas/lectures/>**

