**I B E D**

# Physiologically structured population models: Formulation, analysis and ecological insights

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# A short biography: André de Roos
## http://staff.fnwi.uva.nl/a.m.deroos

- Ecologist with a strong interest understanding how ecological systems *function* (*dynamics*) and (some) mathematical skills

- PhD in Theoretical Biology at Leiden University (1989)
  *Supervisors*: **Hans Metz** and **Odo Diekmann**
  *Topic*:  Numerical methods of physiologically structured population models (*Escalator Boxcar Train)*

  *an EBT implementation with adaptive spacing of cohort introduction times .... offers the best  overall performance for SSPMs*                Zhang, Dieckmann, Brännström, 2017

- Nowadays: using state-of-the-art (numerical) toolbox (dynamics, bifurcation analysis, adaptive dynamics) for studying dynamics of structured population models (PSPMs) to *answer ecological and evolutionary questions*

- In case of PSPMs *biology has driven the mathematical progress*
  ⇒    **Do not blindly apply existing methods from mathematics or physics, think carefully about your biological system first**

# Overview of lectures

- **Lecture 1:** Conceptual, (somewhat) mathematical, the basic idea

- **Lecture 2:** Counterintuitive implications for ecological community structure

- **Lecture 3:** General formulation of a PSPM, numerical tools and techniques

- **Lecture 4:** Implications for ecological dynamics



Population and Community Ecology of Ontogenetic Development

André M. de Roos and Lennart Persson

MONOGRAPHS IN POPULATION BIOLOGY · 51

**Population and Community Ecology of Ontogenetic Development**
André M. de Roos & Lennart Persson
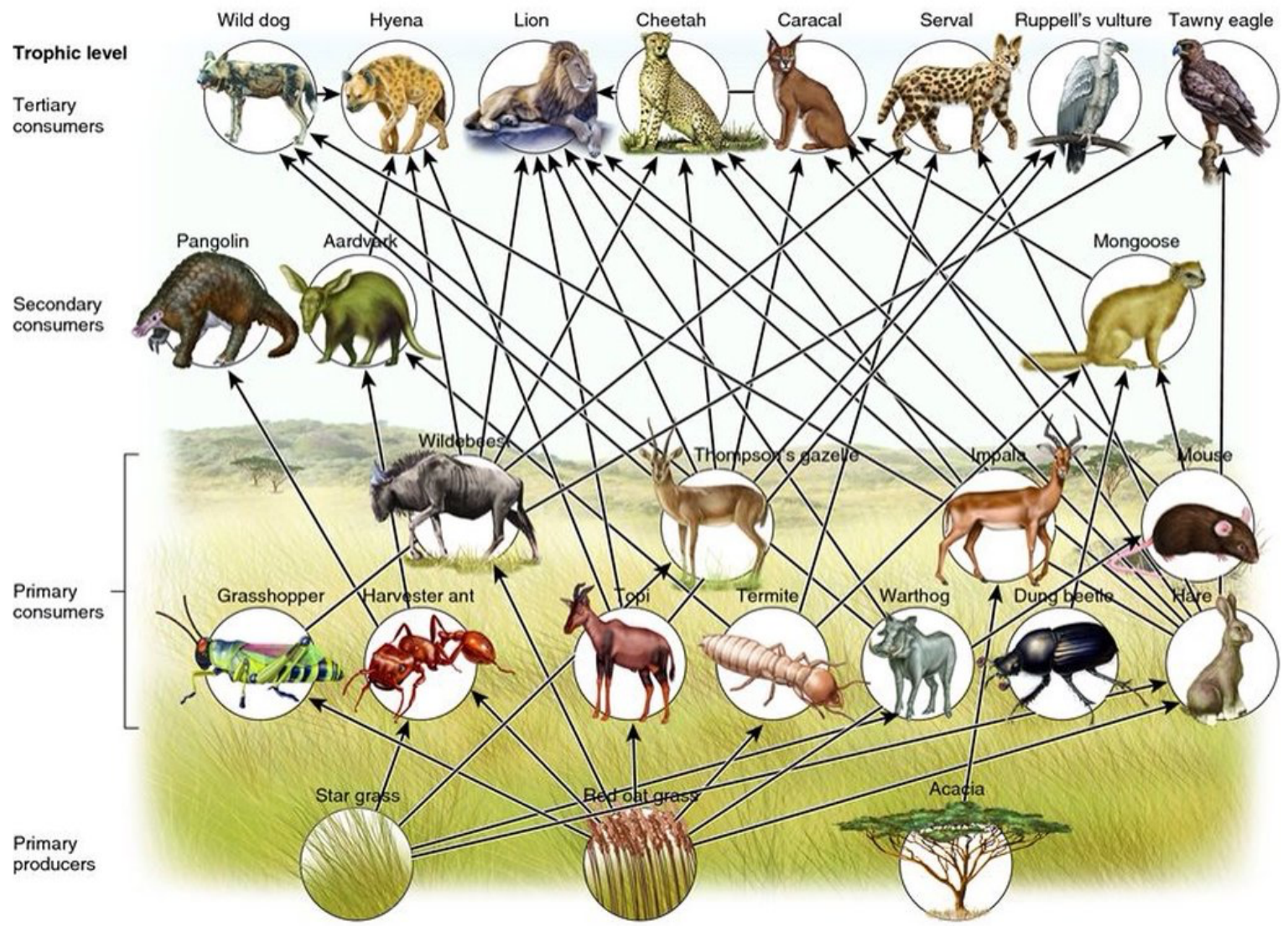Princeton Monographs 51



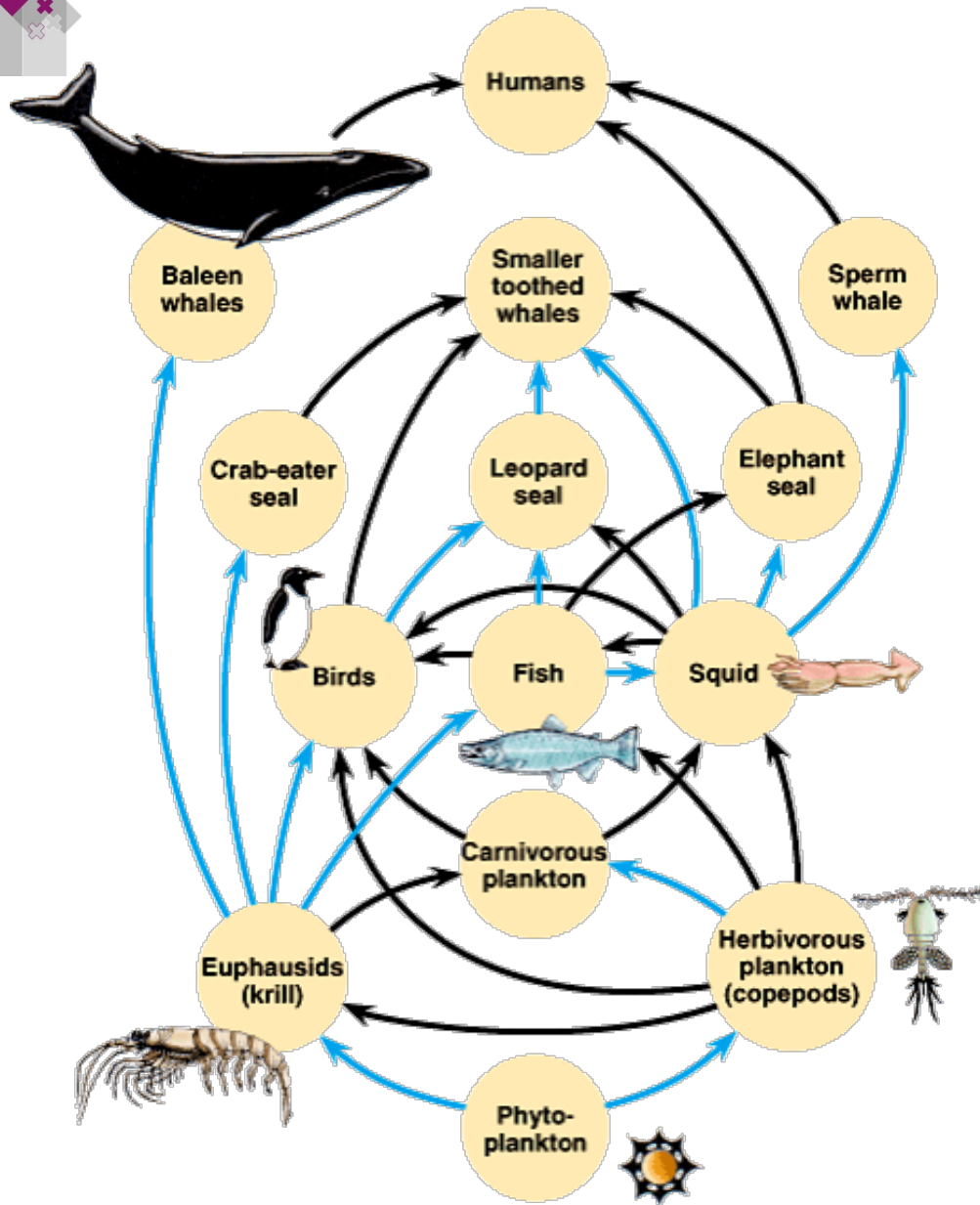**André de Roos**   **Lennart Persson**

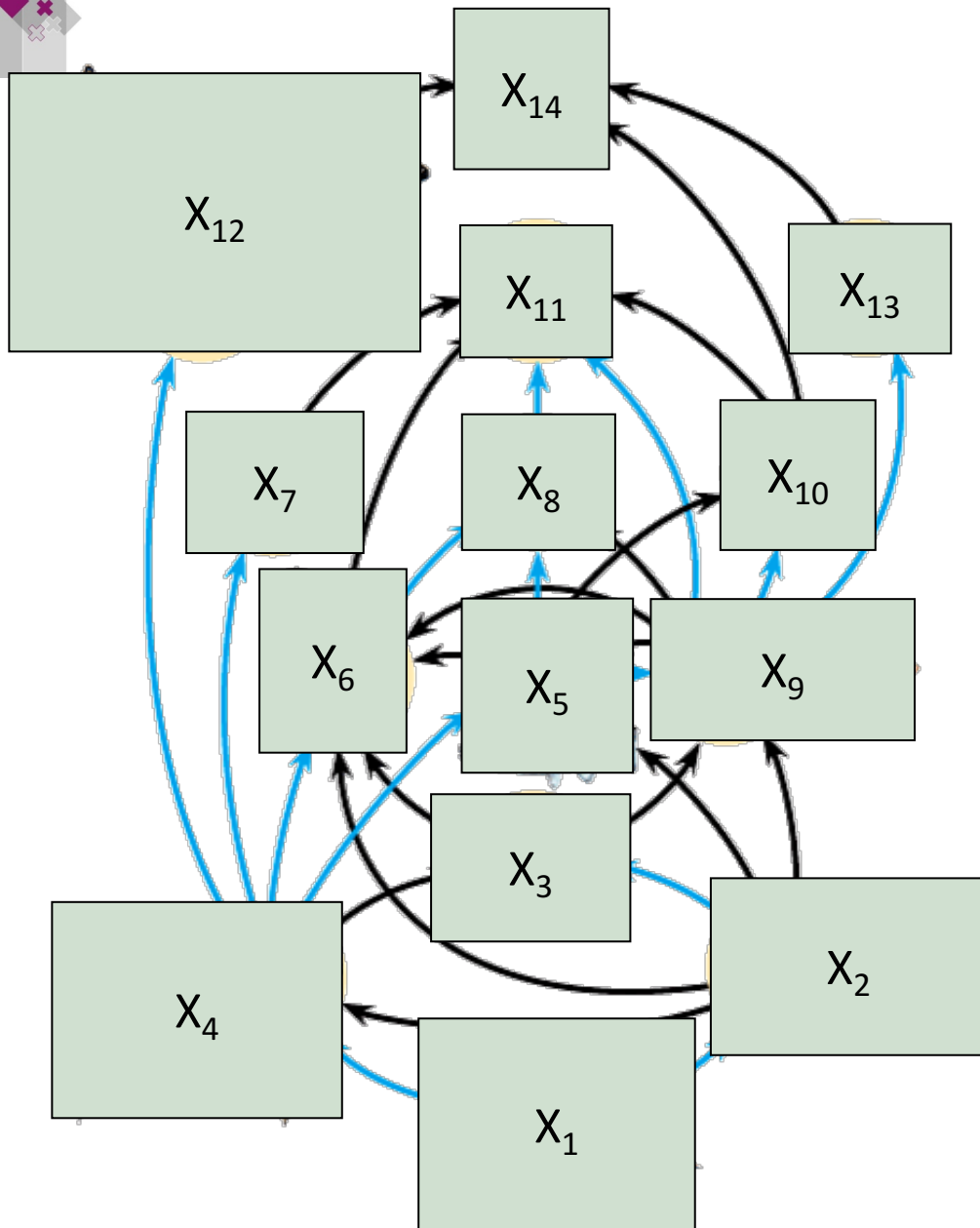# Ecology is all about interactions

# Modeling ecological dynamics

# Modeling ecological dynamics



Alfred Lotka          Vito Volterra

$$\frac{dx_i}{dt} = g(x_1, \ldots, x_n)$$

$$i = 1, \ldots, n$$

# Dynamics of interacting populations

"*Population dynamics: the variations in time and space in the sizes and densities of populations (the **numbers of individuals** per unit area)*"

M.Begon, C.R.Townsend, J.L.Harper (2005)
Ecology: From Individuals to Populations, Wiley-Blackwell

## Is there a problem?

Populations considered as **collections of elementary particles**, only increasing and decreasing in abundance through **reproduction and mortality**, respectively

# A "general" predator-prey model

$$
\begin{cases}
\dfrac{dR}{dt} = p(R) - f(R)\,C \\[2ex]
\dfrac{dC}{dt} = \epsilon f(R)C - \mu C
\end{cases}
$$

$$f'(R) > 0$$

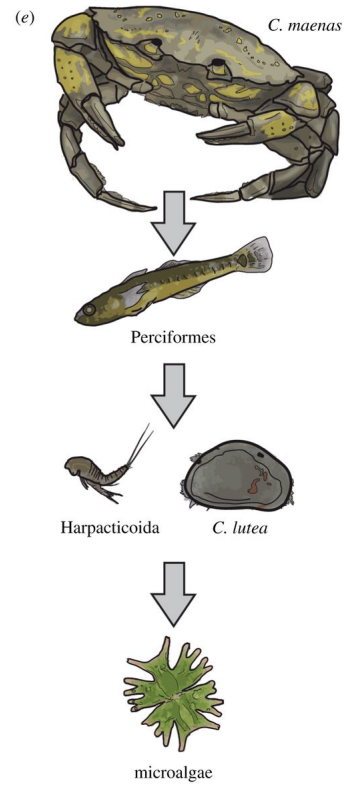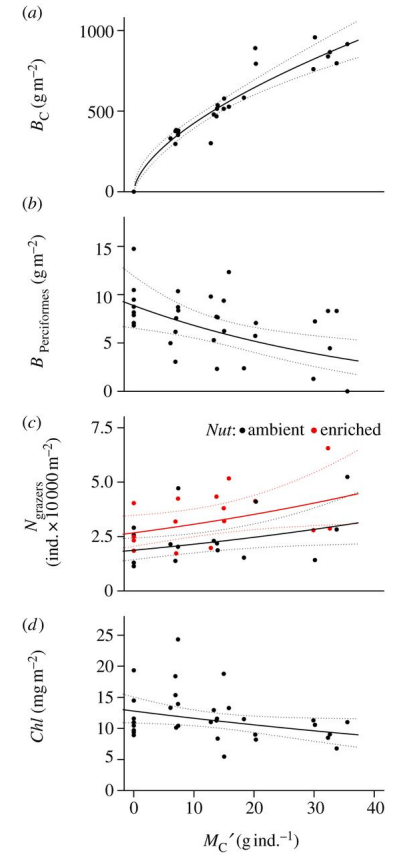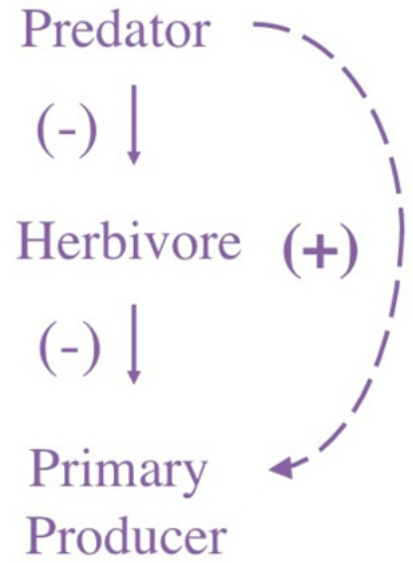Considered to be "general" because it "captures the bare essence of the predator-prey interaction"

**Two fundamental predictions:**

- Equilibrium consumer density decreases with increasing consumer mortality

- Limit cycles occur under a wide range of conditions if $p'(R) \geq 0$ (e.g. exponential or logistic prey growth)
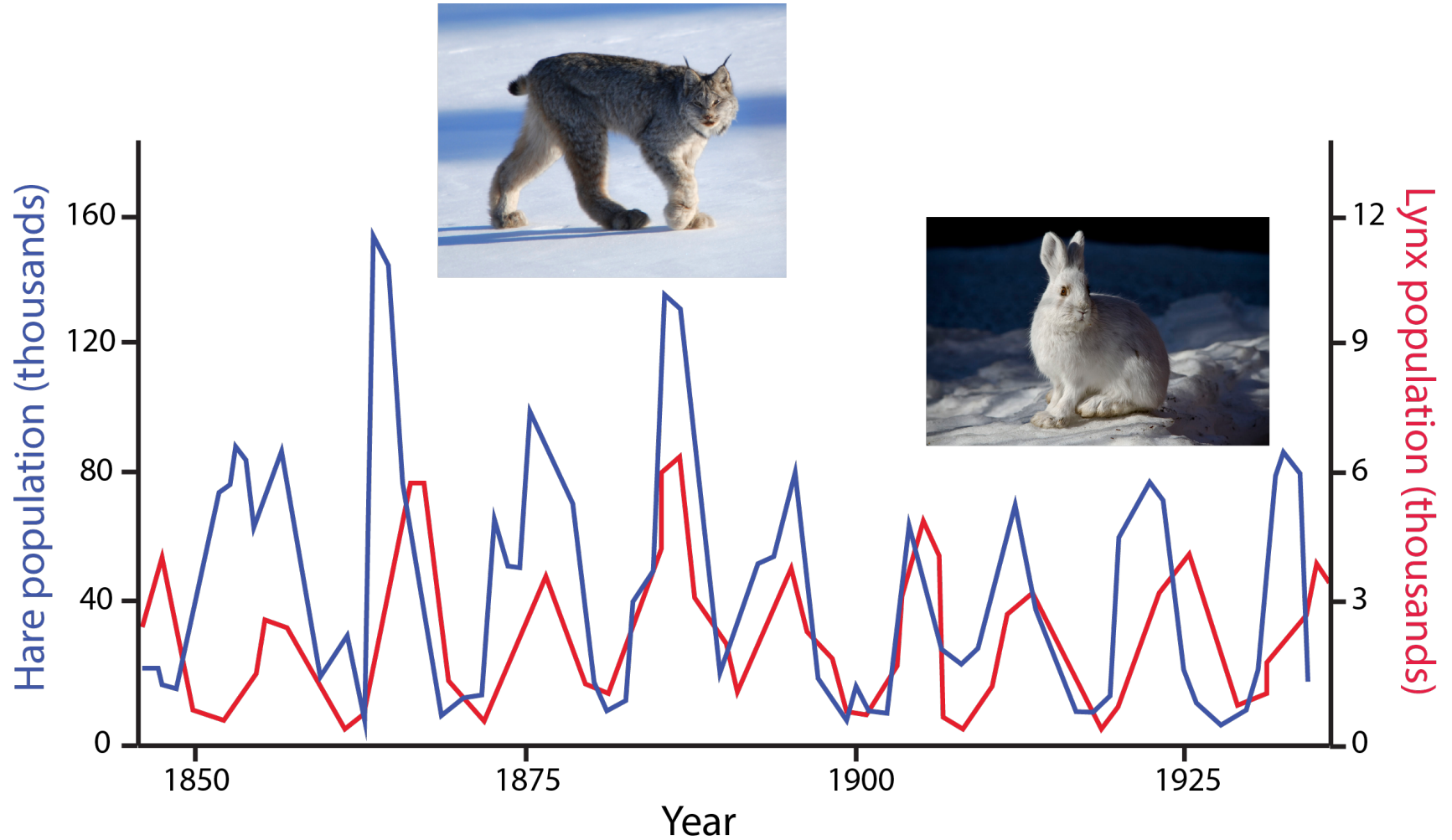
# Food chains: trophic cascades



**Longer food chains due to:**

- Increased resource productivity

- Decreased exploitation of top predator

# Predator-prey dynamics: cycles abound....

# ... or perhaps not?

**Table 1** Distribution of periodic and nonperiodic populations and species among taxonomic classes of animals. Confidence intervals are based on the binomial likelihood function of the true probability given the observed incidence and sample size. Under species, the "raw" classification includes every species with at least one cyclic population; in the "Bonferroni" classification the critical significance level is divided by the number of populations in the species

| | Populations | | | Species | | |
|---|---|---|---|---|---|---|
| | | | | | Fraction periodic (95% CI) | |
| Taxon | Number | Number periodic | Fraction periodic (95% CI) | Number | Raw | Bonferroni |
| Birds | 139 | 18 | 0.13 (0.08, 0.20) | 89 | 0.18 (0.11, 0.27) | 0.16 (0.10, 0.25) |
| Mammals | 328 | 109 | 0.33 (0.28, 0.39) | 27 | 0.70 (0.51, 0.84) | 0.48 (0.31, 0.66) |
| Fish | 129 | 56 | 0.43 (0.35, 0.52) | 27 | 0.70 (0.51, 0.84) | 0.63 (0.44, 0.78) |
| Insects | 79 | 13 | 0.16 (0.10, 0.26) | 68 | 0.17 (0.10, 0.28) | 0.16 (0.09, 0.27) |
| Crustaceans | 12 | 6 | 0.50 (0.25, 0.75) | 3 | 0.33 (0.07, 0.81) | 0.33 (0.07, 0.81) |
| Gastropods | 3 | 1 | 0.33 (0.07, 0.81) | 3 | 0.33 (0.07, 0.81) | 0.33 (0.07, 0.81) |
| Bivalves | 3 | 1 | 0.33 (0.07, 0.81) | 3 | 0.33 (0.07, 0.81) | 0.33 (0.07, 0.81) |
| All populations | 694 | 204 | 0.29 (0.26, 0.33) | 220 | 0.31 (0.26, 0.38) | 0.26 (0.21, 0.33) |

**30% of 700 populations cycle
(mainly fish and mammals)**

Kendall et al. *Ecol. Letters* 1: 160-164 (1998)

# Classic predator-prey cycles are not common
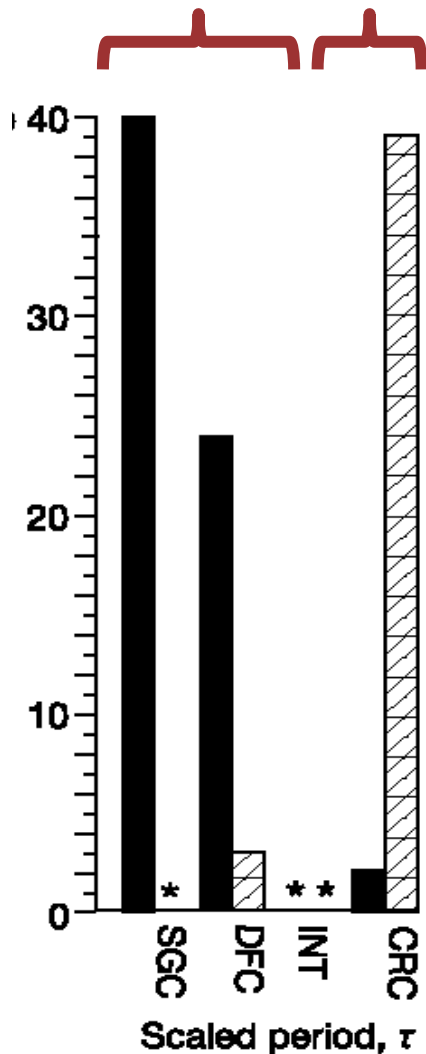


Scaled period, $\tau$

Distribution of cycles among classes defined by scaled period.

- SGC, single-generation cycles ($\tau = 1$)
- DFC, delayed-feedback cycles ($2 \leq \tau \leq 4$)
- CRC, consumer–resources cycles (period in years $4\,T_C + 2\,T_R$ )

No cycles fall in the intermediate class (INT) between single-species and consumer–resource cycles

**The majority of observed population cycles are *not* predator-prey cycle**

Murdoch et al. (2002) *Nature* 417: 541-543

# A "general" predator-prey model

$$
\begin{cases}
\dfrac{dR}{dt} = p(R) - f(R)\,C \\[2em]
\dfrac{dC}{dt} = \epsilon f(R)C - \mu C
\end{cases}
$$

$$
f'(R) > 0
$$

These unstructured, Lotka-Volterra-type models underlie our thinking and theory about ecological systems

**But these models completely ignores the bare essence of life:**

- Individuals have to develop and growth in size before they can contribute to further population growth
  (juvenile-adult stage structure, juvenile delay)

- Mere existing costs energy
  (maintenance costs)

# Today's special

How **juvenile-adult stage-structure** and **maintenance requirements** overturn fundamental ecological insights derived from unstructured models

# The archetypical consumer-resource model

$$
\begin{cases}
\dfrac{dR}{dt} = p(R) - f(R)C \\[2ex]
\dfrac{dC}{dt} = g(R)C - \mu C
\end{cases}
$$

$$\boxed{p'(R) \leq 0} \quad \text{and} \quad f'(R), g'(R) > 0$$

**Two fundamental predictions:**

- Equilibrium consumer density decreases with increasing mortality

- Equilibrium is always stable (no limit cycles)

# Simple stage-structure

$$
\begin{cases}
\dfrac{dR}{dt} & = \; p(R) \; - \; f_J(R)C_J \; - \; f_A(R)C_A \\[2mm]
\dfrac{dC_J}{dt} & = \; g_A(R)C_A \; - \; g_J(R)C_J \; - \; \mu_J C_J \\[2mm]
\dfrac{dC_A}{dt} & = \; g_J(R)C_J \; - \; \mu_A C_A
\end{cases}
$$

$$
p'(R) \; \leq \; 0 \quad \text{and} \quad f'_J(R), f'_A(R), g'_J(R), g'_A(R) > 0
$$

# When structure does not matter at all

$$f_J(R) = \alpha_J f(R), \qquad\qquad f_A(R) = \alpha_A f(R)$$

$$g_J(R) = \gamma g(R), \qquad\qquad g_A(R) = \beta g(R)$$

$$\mu_J = \mu_A = \mu$$

Define $C = C_J + C_A$ and $z = C_J/(C_J + C_A)$

$$
\begin{aligned}
\frac{dC}{dt} &= g_A(R)C_A - \mu_J C_J - \mu_A C_A \\
&= g_A(R)(1-z)C - \mu_J z C - \mu_A(1-z)C
\end{aligned}
$$

# When structure does not matter at all

Define $C = C_J + C_A$ and $z = C_J/(C_J + C_A)$

$$\frac{dC}{dt} = g_A(R)C_A - \mu_J C_J - \mu_A C_A$$

$$= g_A(R)(1-z)C - \mu_J zC - \mu_A(1-z)C$$

$$\frac{dz}{dt} = \frac{1}{C_J + C_A}\frac{dC_J}{dt} - \frac{C_J}{C_J + C_A}\frac{1}{C_J + C_A}\frac{d(C_J + C_A)}{dt}$$

$$= g_A(R)(1-z) - g_J(R)z - \mu_J z$$

$$\qquad - z\left(g_A(R)(1-z) - \mu_J z - \mu_A(1-z)\right)$$

$$= g_A(R)(1-z)^2 - g_J(R)z - (\mu_J - \mu_A)\,z(1-z)$$

# When structure does not matter at all

$$
\begin{cases}
\dfrac{dR}{dt} = p(R) - \left(\alpha_J z + \alpha_A(1-z)\right) f(R)C \\[2ex]
\dfrac{dC}{dt} = \beta g(R)(1-z)C - \mu C \\[2ex]
\dfrac{dz}{dt} = \left(\beta(1-z)^2 - \gamma z\right) g(R)
\end{cases}
$$

For $t \to \infty$ $z$ will always approach its equilibrium value $\bar{z}$:

$$
\beta(1-\bar{z})^2 - \gamma\bar{z} = 0 \quad \Rightarrow \quad \bar{z} = \left(1 + \frac{\gamma}{2\beta} - \sqrt{\left(1 + \frac{\gamma}{2\beta}\right)^2 - 1}\right)
$$

# When structure does not matter at all

$$\begin{cases} \dfrac{dR}{dt} = p(R) - \bar{\alpha} f(R) C \\ \dfrac{dC}{dt} = \bar{\beta} g(R) C - \mu C \end{cases}$$

in which $\bar{\alpha} = \alpha_J \bar{z} + \alpha_A (1 - \bar{z})$ and $\bar{\beta} = \beta (1 - \bar{z})$.

**Necessary assumptions:**

- Ingestion and production (maturation, reproduction) have the same dependence on resource density (but *not* stage-independent)

- Mortality rate is the same for both stages

**Generalizable to arbitrarily many stages!**

# The effects of stage-structure alone

- Common assumption: numerical response is proportional to functional response:

$$
\begin{cases}
\dfrac{dR}{dt} &= p(R) - f_J(R)C_J - f_A(R)C_A \\[2mm]
\dfrac{dC_J}{dt} &= \beta\, f_A(R)C_A - \gamma\, f_J(R)C_J - \mu_J C_J \\[2mm]
\dfrac{dC_A}{dt} &= \gamma\, f_J(R)C_J - \mu_A C_A
\end{cases}
$$

$$p'(R) \le 0 \quad \text{and} \quad f'_J(R), f'_A(R) > 0 \quad (\text{but not } f_J(R) \propto f_A(R))$$

# Unique equilibrium state

$$
\begin{cases}
H_1(\bar{R}, \bar{C}_J, \bar{C}_A) \;=\; p(\bar{R}) \;-\; f_J(\bar{R})\bar{C}_J \;-\; f_A(\bar{R})\bar{C}_A & =\; 0 \\[2ex]
H_2(\bar{R}, \bar{C}_J, \bar{C}_A) \;=\; \beta f_A(\bar{R})\bar{C}_A \;-\; \gamma f_J(\bar{R})\bar{C}_J \;-\; \mu_J \bar{C}_J & =\; 0 \\[2ex]
H_3(\bar{R}, \bar{C}_J, \bar{C}_A) \;=\; \gamma f_J(\bar{R})\bar{C}_J \;-\; \mu_A \bar{C}_A & =\; 0
\end{cases}
$$

$$
\Rightarrow \quad
\begin{cases}
\gamma f_J(\bar{R})\left(\beta f_A(\bar{R}) \;-\; \mu_A\right) \;-\; \mu_J \mu_A \;=\; 0 \\[3ex]
\bar{C}_J \;=\; \dfrac{p(\bar{R})}{f_J(\bar{R})\left(1 \;+\; \gamma f_A(\bar{R})/\mu_A\right)} \\[4ex]
\bar{C}_A \;=\; \dfrac{\gamma p(\bar{R})}{\mu_A \;+\; \gamma f_A(\bar{R})}
\end{cases}
$$

# The effects of stage-structure alone

In a 3-dimensional ODE system a unique, positive equilibrium state ensures that $D = \det J < 0$

$$J = \begin{pmatrix} p'(\bar{R}) - f'_J(\bar{R})\bar{C}_J - f'_A(\bar{R})\bar{C}_A & -f_J(\bar{R}) & -f_A(\bar{R}) \\ \beta f'_A(\bar{R})\bar{C}_A - \gamma f'_J(\bar{R})\bar{C}_J & -\gamma f_J(\bar{R}) - \mu_J & \beta f_A(\bar{R}) \\ \gamma f'_J(\bar{R})\bar{C}_J & \gamma f_J(\bar{R}) & -\mu_A \end{pmatrix}$$

$$D = -\left(\gamma f_A(\bar{R}) + \mu_A\right)\left(\mu_J f'_J(\bar{R})\bar{C}_J + \beta f_J(\bar{R})f'_A(\bar{R})\bar{C}_A\right)$$

# The effects of stage-structure alone

- Changes in equilibrium density can be assessed using the implicit function theorem:

$$
\begin{pmatrix}
\dfrac{\partial H_1}{\partial R} & \dfrac{\partial H_1}{\partial \bar{C}_J} & \dfrac{\partial H_1}{\partial \bar{C}_A} \\[2.5ex]
\dfrac{\partial H_2}{\partial R} & \dfrac{\partial H_2}{\partial \bar{C}_J} & \dfrac{\partial H_2}{\partial \bar{C}_A} \\[2.5ex]
\dfrac{\partial H_3}{\partial R} & \dfrac{\partial H_3}{\partial \bar{C}_J} & \dfrac{\partial H_3}{\partial \bar{C}_A}
\end{pmatrix}
\begin{pmatrix}
\dfrac{d\bar{R}}{d\mu_J} \\[2.5ex]
\dfrac{d\bar{C}_J}{d\mu_J} \\[2.5ex]
\dfrac{d\bar{C}_A}{d\mu_J}
\end{pmatrix}
+
\begin{pmatrix}
0 \\[2.5ex]
-\bar{C}_J \\[2.5ex]
0
\end{pmatrix}
= 0
$$

$$
\Rightarrow \quad J
\begin{pmatrix}
\dfrac{d\bar{R}}{d\mu_J} \\[2.5ex]
\dfrac{d\bar{C}_J}{d\mu_J} \\[2.5ex]
\dfrac{d\bar{C}_A}{d\mu_J}
\end{pmatrix}
=
\begin{pmatrix}
0 \\[2.5ex]
\bar{C}_J \\[2.5ex]
0
\end{pmatrix}
$$

# The effects of stage-structure alone

$$\frac{d\bar{C}_J}{d\mu_J} = D^{-1} \begin{vmatrix} p'(\bar{R}) - f'_J(\bar{R})\bar{C}_J - f'_A(\bar{R})\bar{C}_A & 0 & -f_A(\bar{R}) \\ \beta f'_A(\bar{R})\bar{C}_A - \gamma f'_J(\bar{R})\bar{C}_J & \bar{C}_J & \beta f_A(\bar{R}) \\ \gamma f'_J(\bar{R})\bar{C}_J & 0 & -\mu_A \end{vmatrix}$$

$$= D^{-1} \left( \mu_A \left( -p'(\bar{R}) + f'_J(\bar{R})\bar{C}_J + f'_A(\bar{R})\bar{C}_A \right) + \gamma f'_J(\bar{R}) f_A(\bar{R}) \bar{C}_J \right) \bar{C}_J$$

$$\Rightarrow \quad \frac{d\bar{C}_J}{d\mu_J} < 0$$

$\dfrac{d\bar{C}_A}{d\mu_J}, \dfrac{d\bar{C}_J}{d\mu_A}$ and $\dfrac{d\bar{C}_A}{d\mu_A}$ are also negative.

# Characteristic equation

$$\begin{vmatrix} p'(\bar{R}) - f'_J(\bar{R})\bar{C}_J - f'_A(\bar{R})\bar{C}_A - \lambda & -f_J(\bar{R}) & -f_A(\bar{R}) \\ \beta f'_A(\bar{R})\bar{C}_A - \gamma f'_J(\bar{R})\bar{C}_J & -\gamma f_J(\bar{R}) - \mu_J - \lambda & \beta f_A(\bar{R}) \\ \gamma f'_J(\bar{R})\bar{C}_J & \gamma f_J(\bar{R}) & -\mu_A - \lambda \end{vmatrix} = 0$$

Analysis is complex, but checking the Routh-Hurwitz criteria reveals that the equilibrium is always stable

**Stage structure alone does not invalidate the fundamental predictions from unstructured consumer resource cycles,** *if the numerical and functional response are proportional*

# Maintenance takes precedence over production
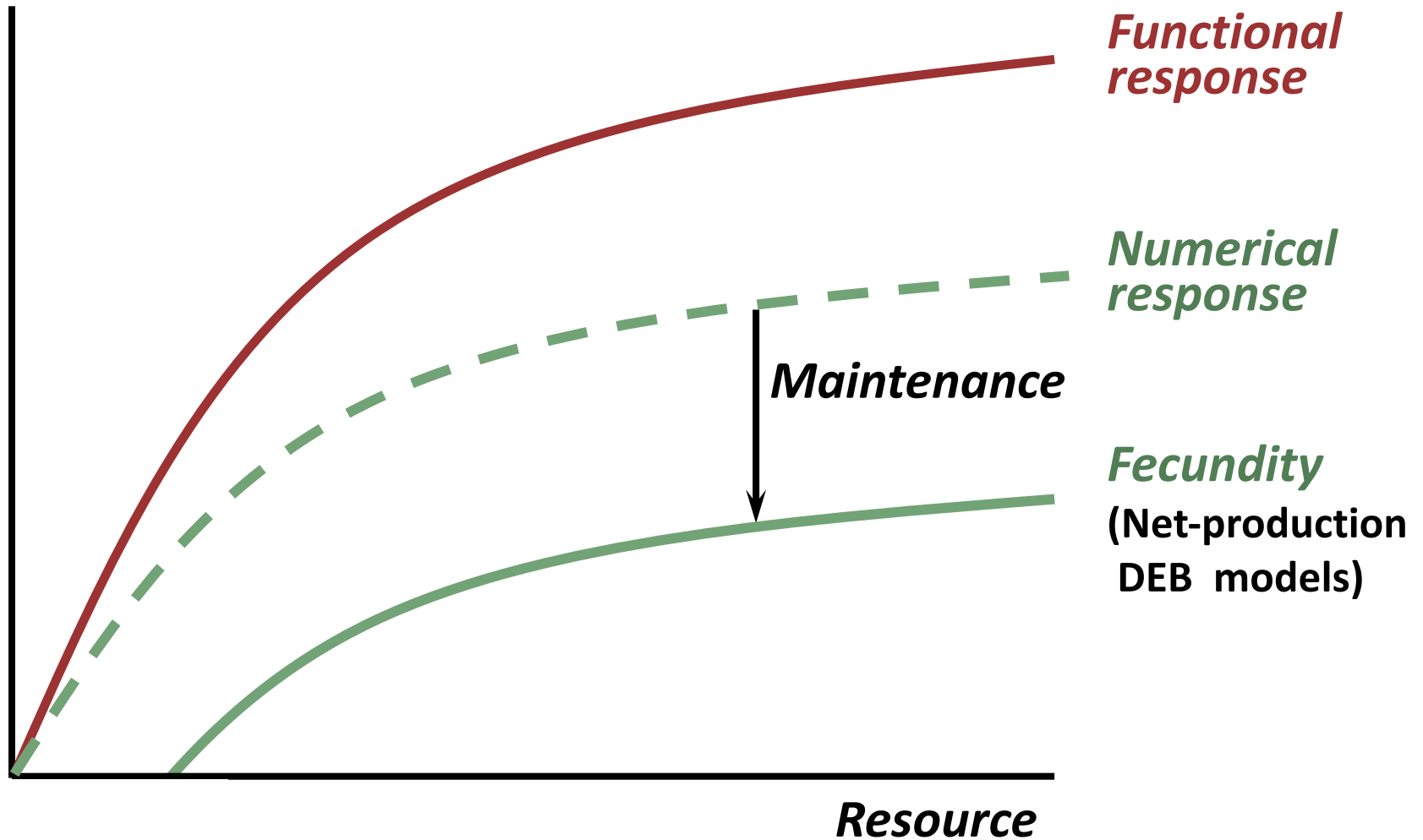
# Maintenance: implicit without stage structure

$$\begin{cases} \dfrac{dR}{dt} = p(R) - f(R)\,C \\[2em] \dfrac{dC}{dt} = (\beta f(R) - T)^+\,C - \mu\,C \end{cases}$$

In the close neighbourhood of an equilibrium state, necessarily:

$$(\beta f(R) - T)^+ = \beta f(R) - T$$

$$\begin{cases} \dfrac{dR}{dt} = p(R) - f(R)\,C \\[2em] \dfrac{dC}{dt} = \beta f(R)C - (\mu + T)\,C \end{cases}$$

# Maintenance and stage structure together

- In equilibrium either juvenile or adult consumer density can increase with increasing mortality (stage-independent, juvenile, adult)

- Population cycles can occur as a consequence of stage-structured dynamics

$$
\begin{cases}
\dfrac{dR}{dt} = P - f(R)\,(C_J + C_A) \\[2mm]
\dfrac{dC_J}{dt} = (\epsilon f(R) - T_A)^+\, C_A - (\epsilon f(R) - T_J)^+\, C_J - \mu\, C_J \\[2mm]
\dfrac{dC_A}{dt} = (\epsilon f(R) - T_J)^+\, C_J - \mu\, C_A
\end{cases}
$$

# Maintenance and stage structure together



Left panel title: $P = \epsilon = T_A = 1, \ T_J = 0.75$

Right panel title: $P = \epsilon = T_A = 1, \ T_J = 1.5$

Y-axis: Juvenile- Adult consumer density

X-axis: Mortality rate $\mu$

Legend:
— Juveniles
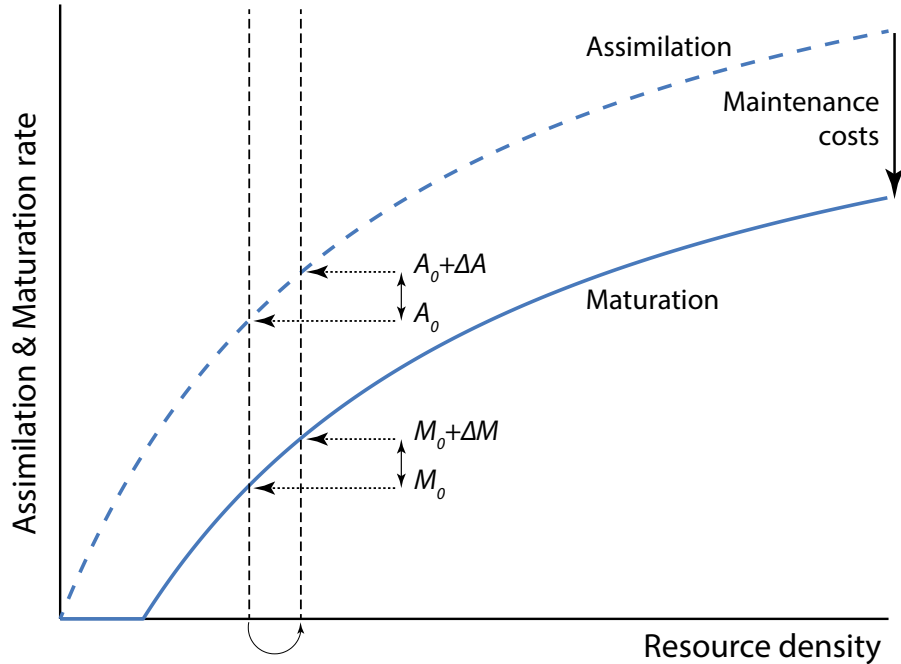-- Adults
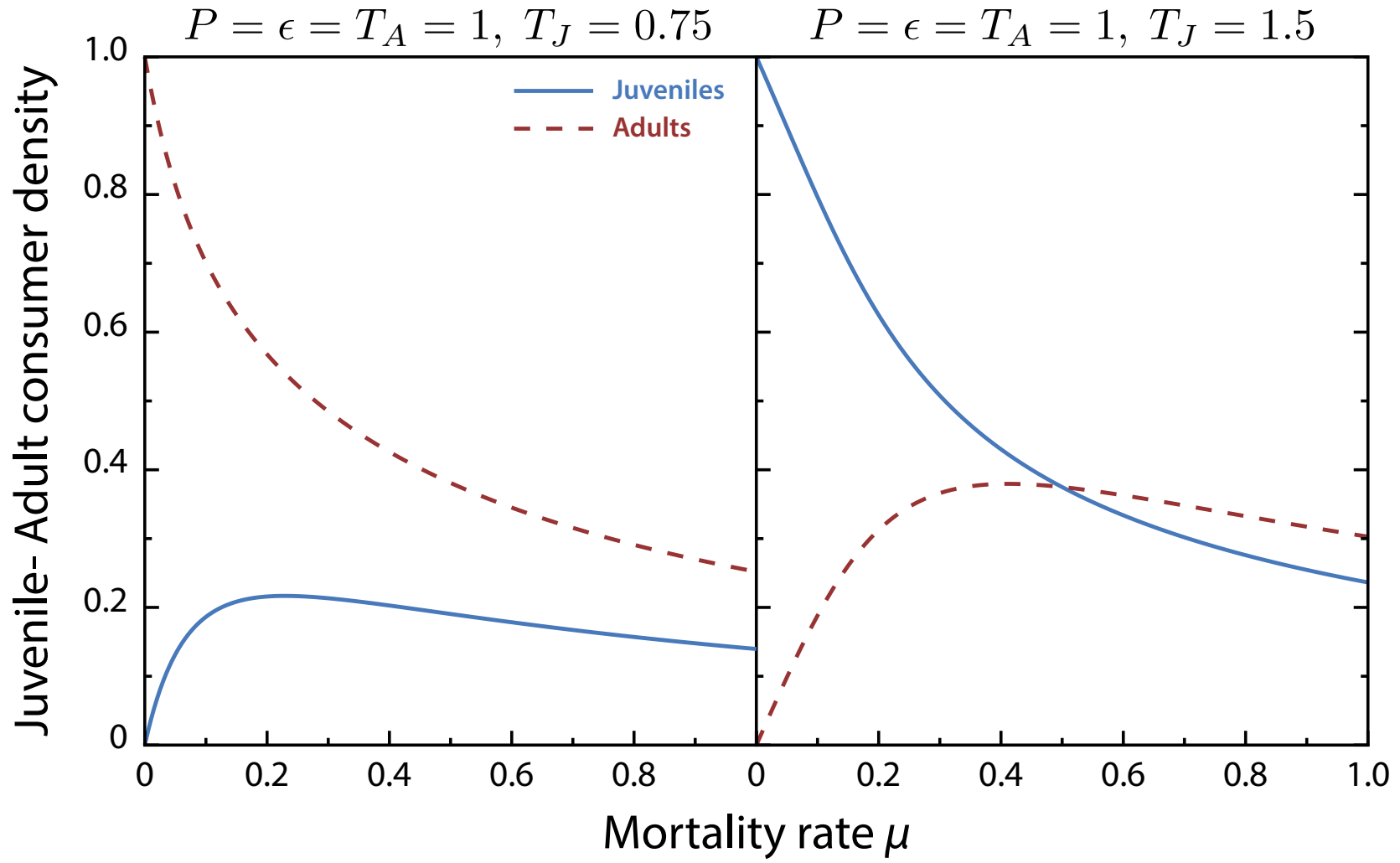
# Maintenance and stage structure together

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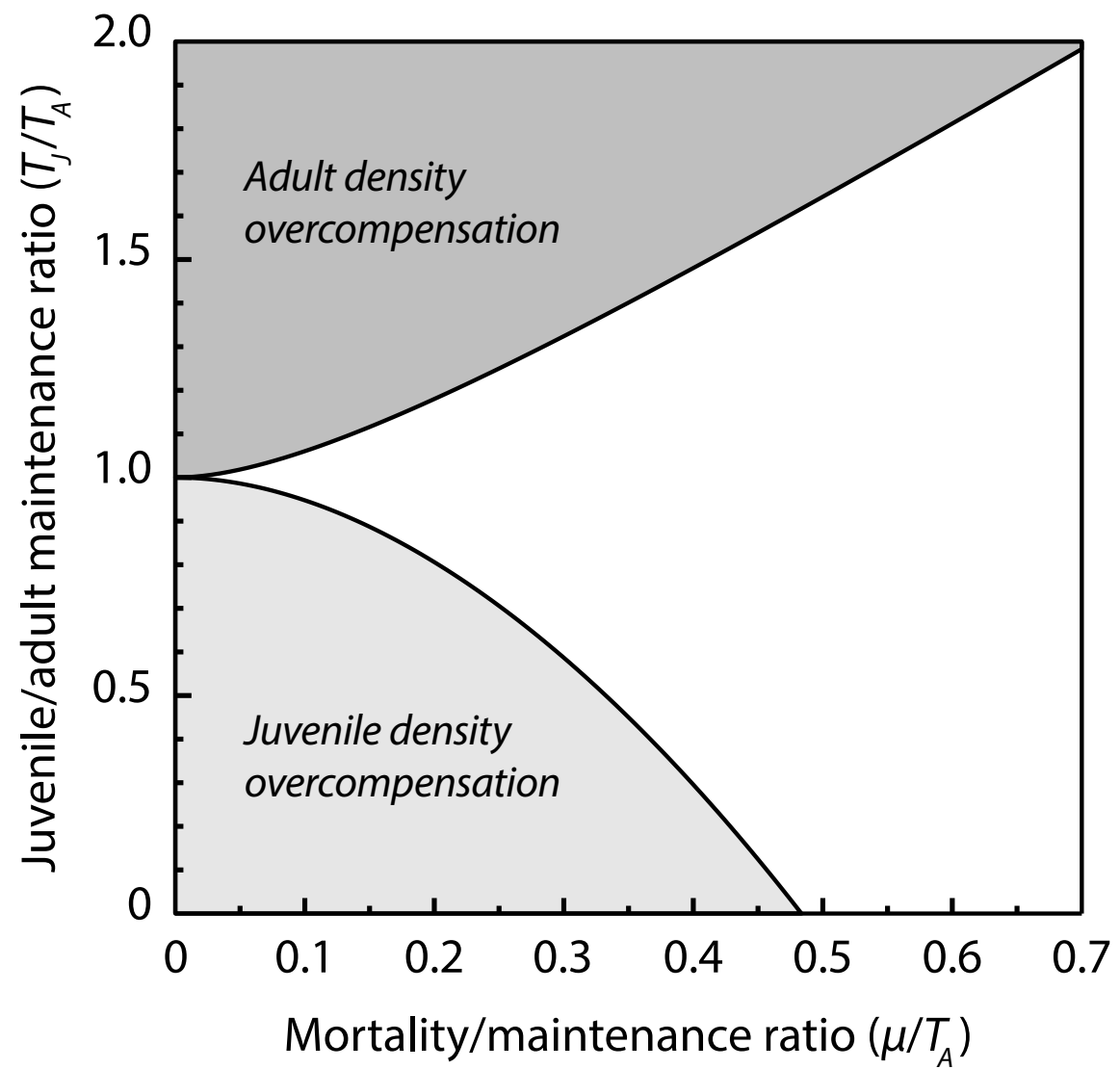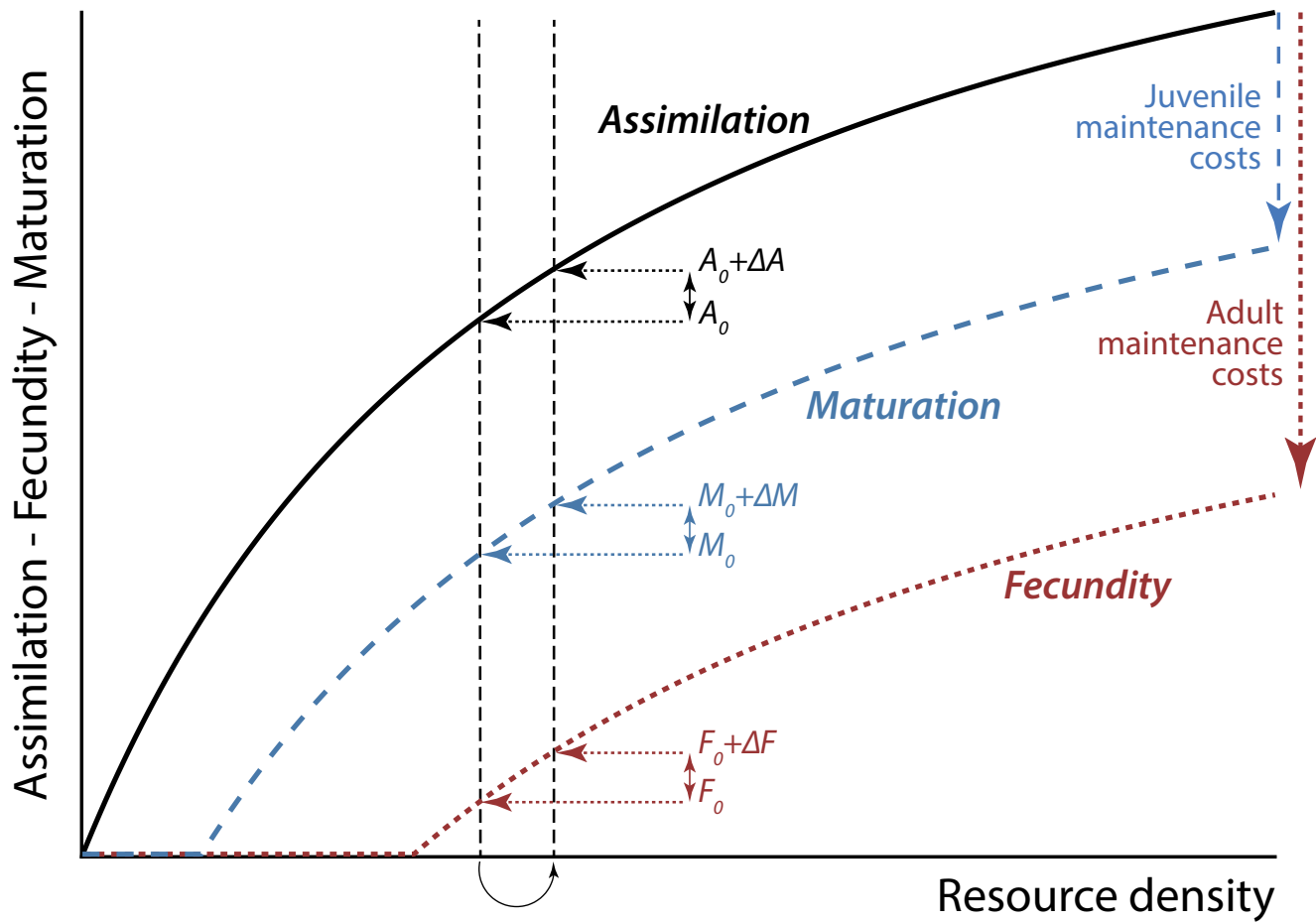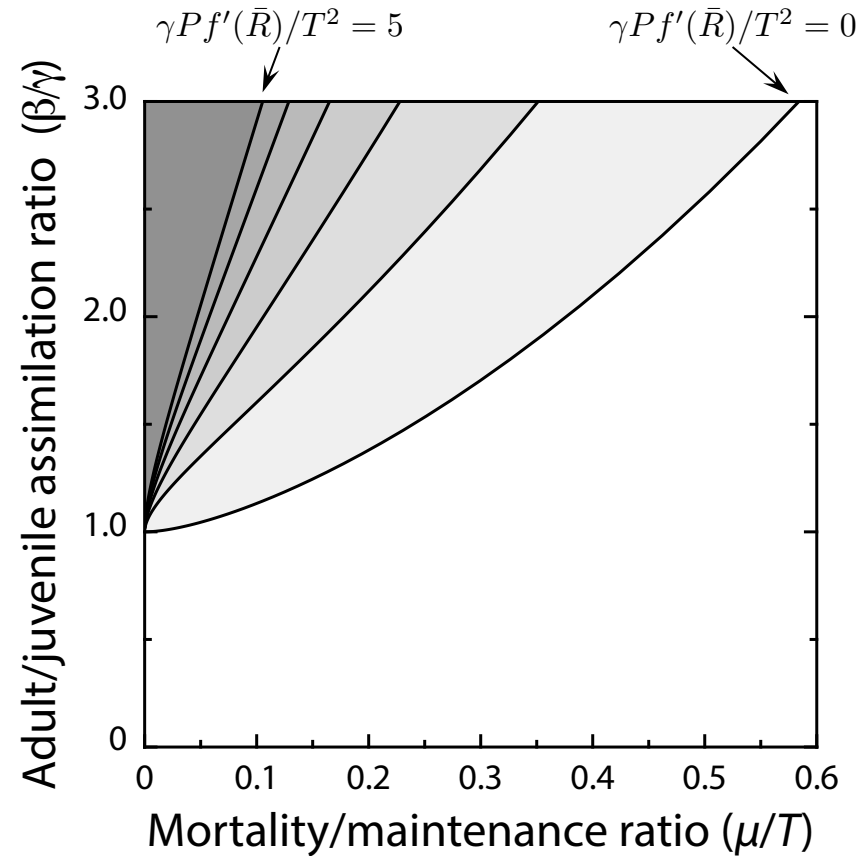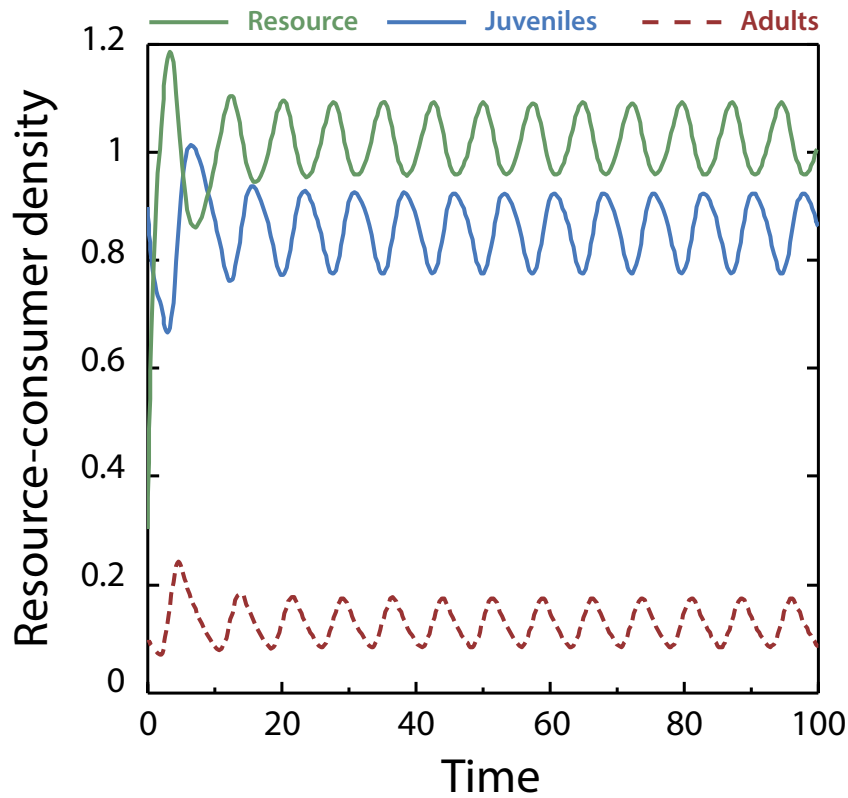


Assimilation increase ≈ 9%  →  Maturation increase ≈ 18%
Reproduction increase ≈ 95%

*Net increase in reproduction >> Net increase in maturation*

# Maintenance and stage structure together
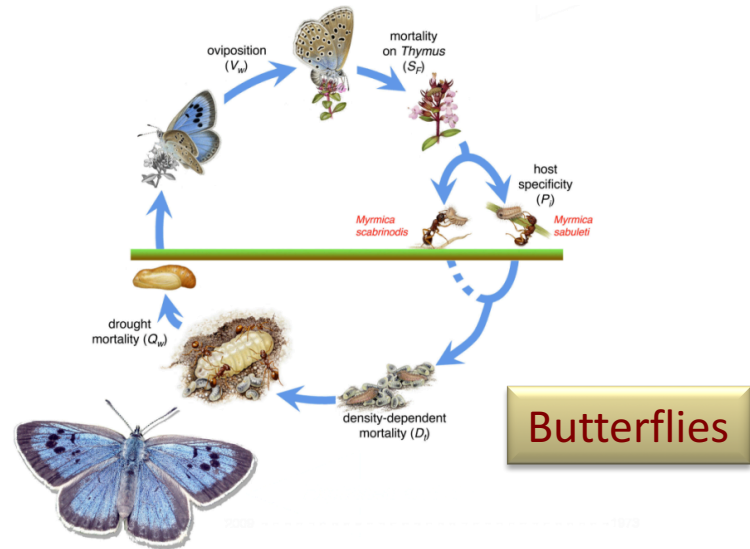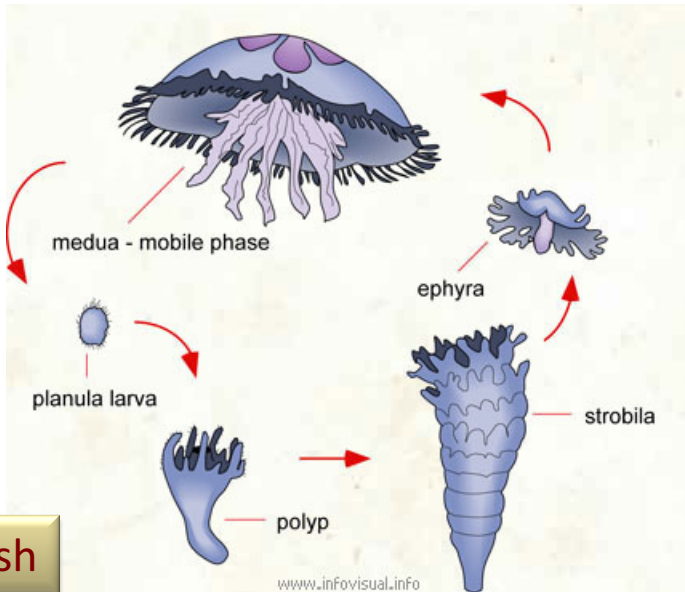


$P = \epsilon = T_A = 1, \ \mu = 0.2, \ T_J = 2.5$
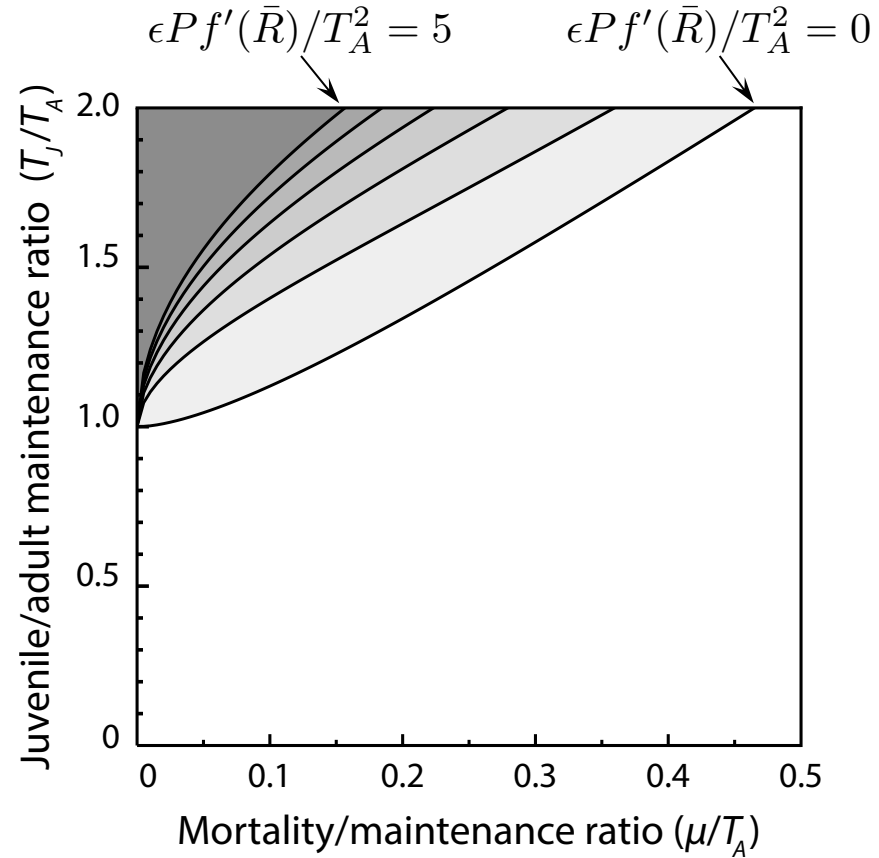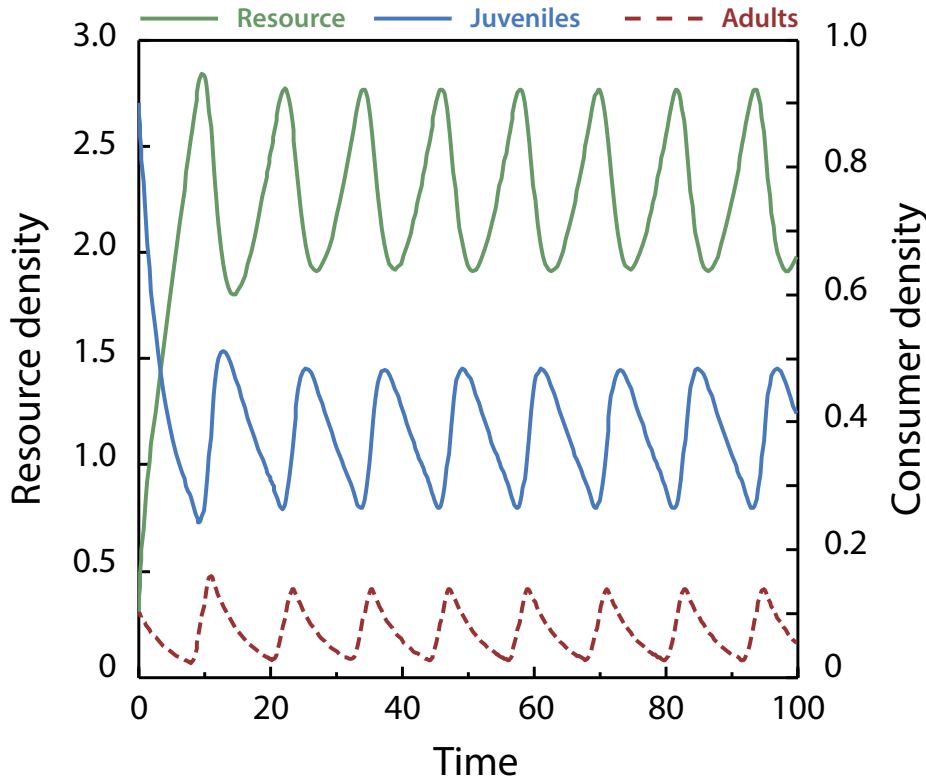
$\epsilon P f'(\bar{R})/T_A^2 = 5$      $\epsilon P f'(\bar{R})/T_A^2 = 0$

# Maintenance and stage structure together

- In equilibrium either juvenile or adult consumer density can increase with increasing mortality (stage-independent, juvenile, adult)

- Population cycles can occur as a consequence of stage-structured dynamics

$$
\begin{cases}
\dfrac{dR}{dt} = P - f(R)\,(C_J + C_A) \\[2ex]
\dfrac{dC_J}{dt} = (\beta f(R) - T)^+\, C_A - (\gamma f(R) - T)^+\, C_J - \mu\, C_J \\[2ex]
\dfrac{dC_A}{dt} = (\gamma f(R) - T)^+\, C_J - \mu\, C_A
\end{cases}
$$

# Maintenance and stage structure together



Left panel title: $P = \gamma = T = 1, \ \beta = 0.75$

Right panel title: $P = \gamma = T = 1, \ \beta = 1.5$

Y-axis: Juvenile- Adult consumer density

X-axis: Mortality rate $\mu$

Legend: Juveniles, Adults

# Maintenance and stage structure together



Figure axes:
- y-axis: Adult/juvenile efficiency ratio ($\beta/\gamma$), from 0 to 3.0
- x-axis: Mortality/maintenance ratio ($\mu/T$), from 0 to 1.0

*Adult density overcompensation*

*Juvenile density overcompensation*

# Maintenance and stage structure together



Assimilation increase ≈ 15%
Maturation increase   ≈ 35%
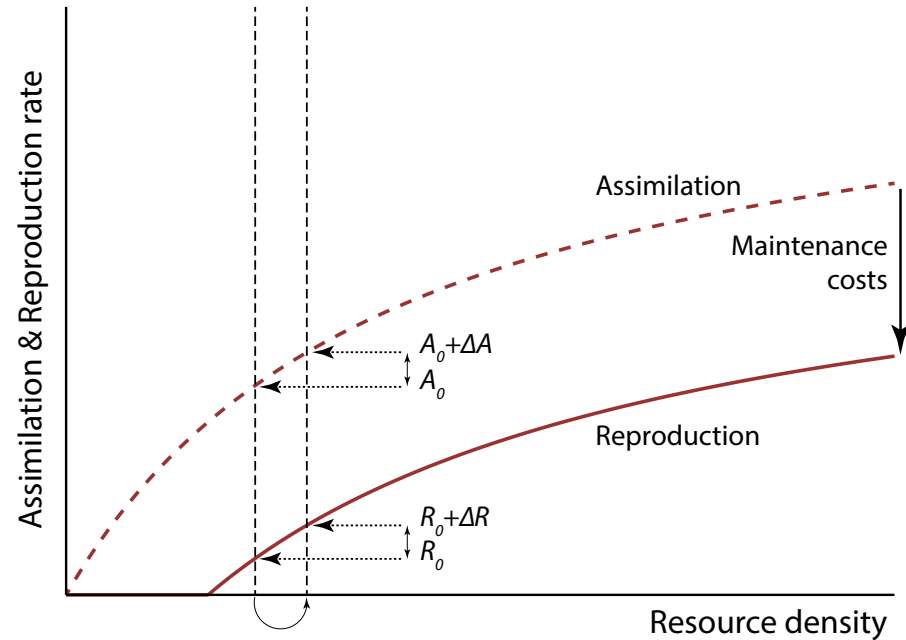
Assimilation increase    ≈ 15%
Reproduction increase ≈ 90%

Net increase in reproduction >> Net increase in maturation

# Maintenance and stage structure together

$P = \gamma = T = 1, \; \beta = 2.5$



Left plot: Resource-consumer density vs Time. Legend: Resource, Juveniles, Adults.

Right plot: Adult/juvenile assimilation ratio ($\beta/\gamma$) vs Mortality/maintenance ratio ($\mu/T$). $\gamma P f'(\bar{R})/T^2 = 5$ and $\gamma P f'(\bar{R})/T^2 = 0$.

# Individual life cycles are complex
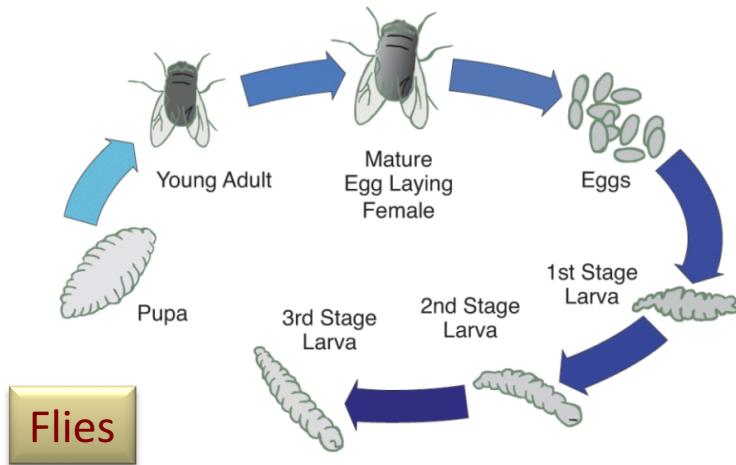


Flies



Butterflies



Jellyfish
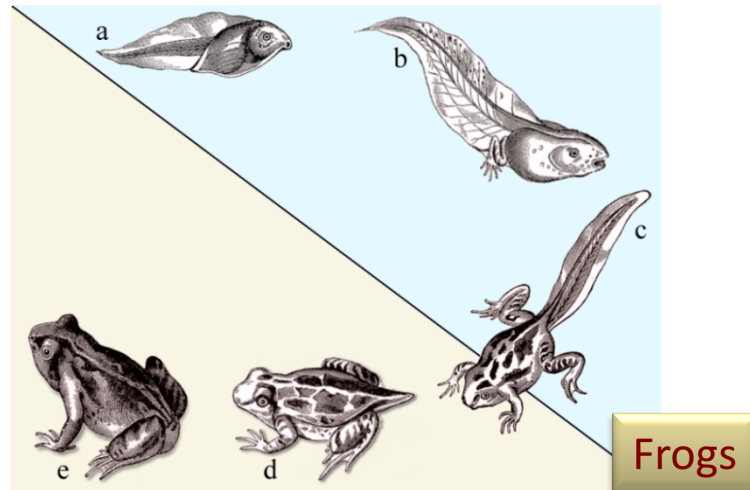


Frogs

**Development predominates!**

# Individual life cycles are complex



Flies

Butterflies

Jellyfish

Frogs
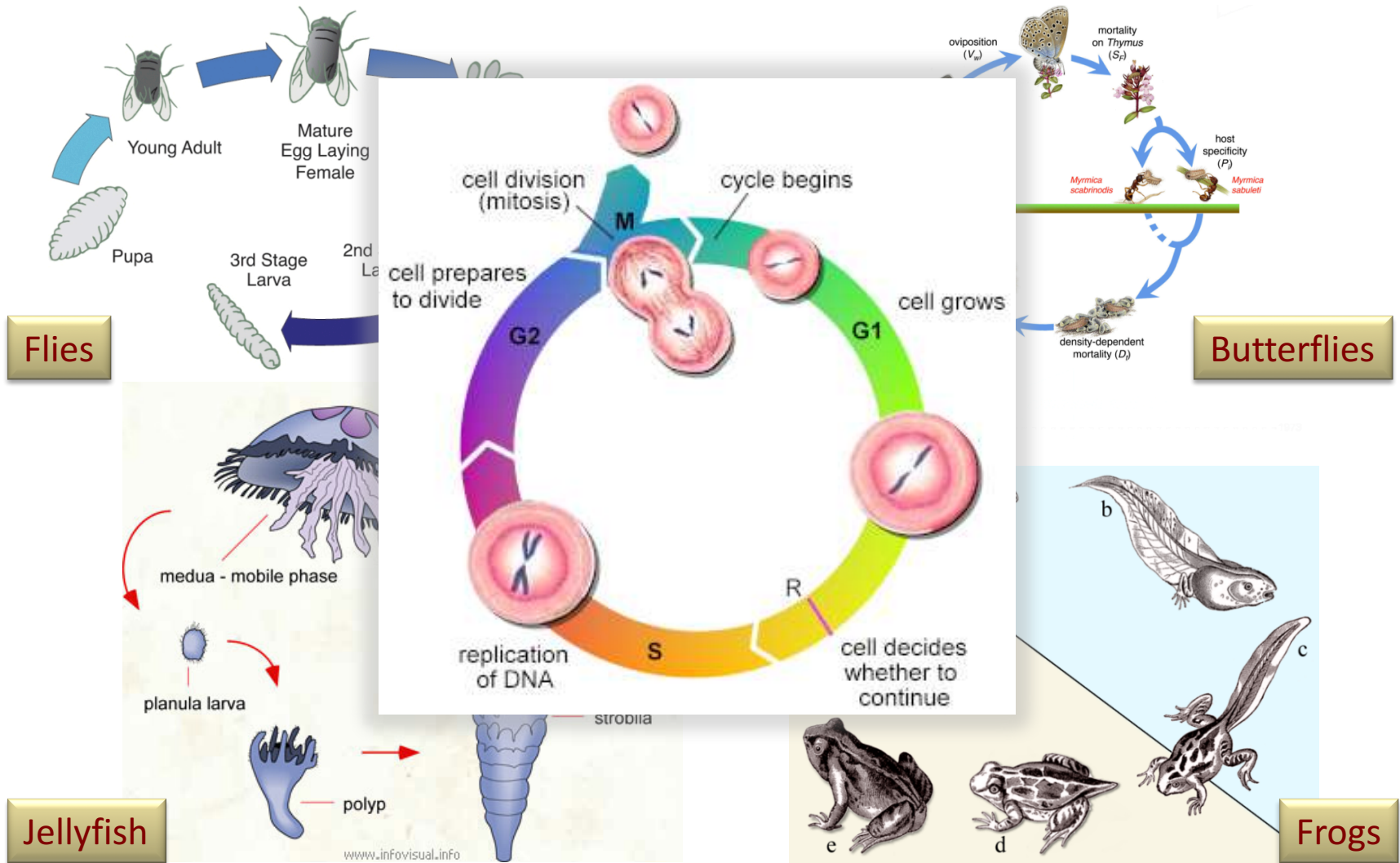
**Development predominates!**

# Life history's most prominent feature: Growth in body size (a doubling at least )



x $10^9$

1 mm

Eggs and Larvae

Juveniles

Adults
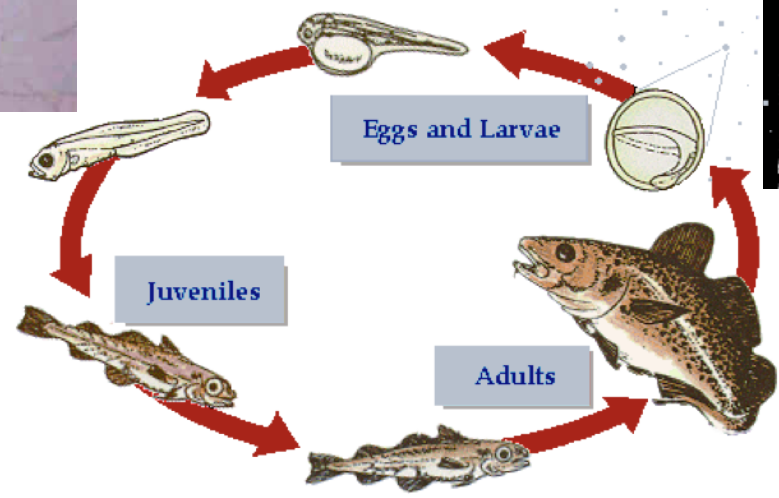
**Intra-specific variation in body size!**

# Life history's most prominent feature: Growth in body size (a doubling at least )



1 mm

All 3 perch are 4 years old!

**Intra-specific variation in body size!**

*Foto by Emma van der Woude*

# Life history's most prominent feature: Growth in body size (a doubling at least )



1 mm

**Intra-specific variation in body size!**
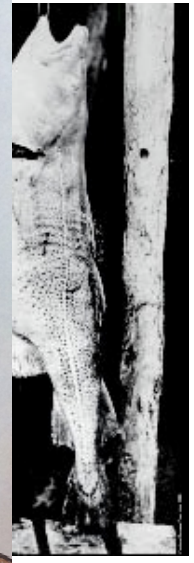
*Foto by Emma van der Woude*

# Food-dependent growth is ubiquitous

~ 1.3 million animal species
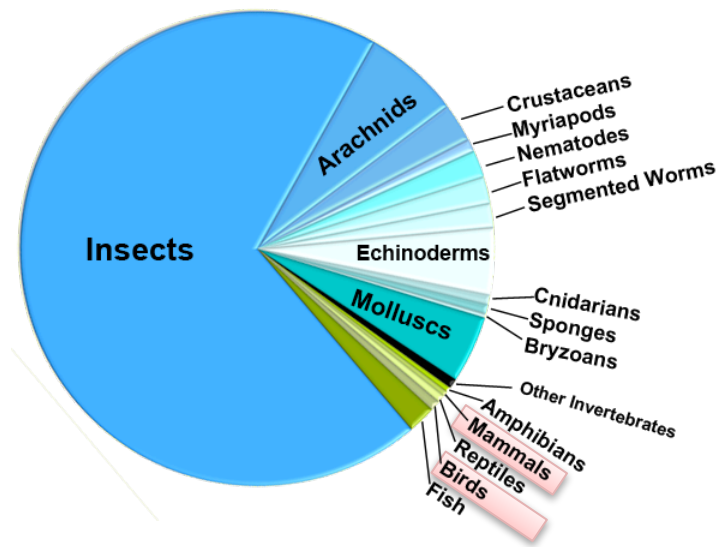
grow substantially after birth
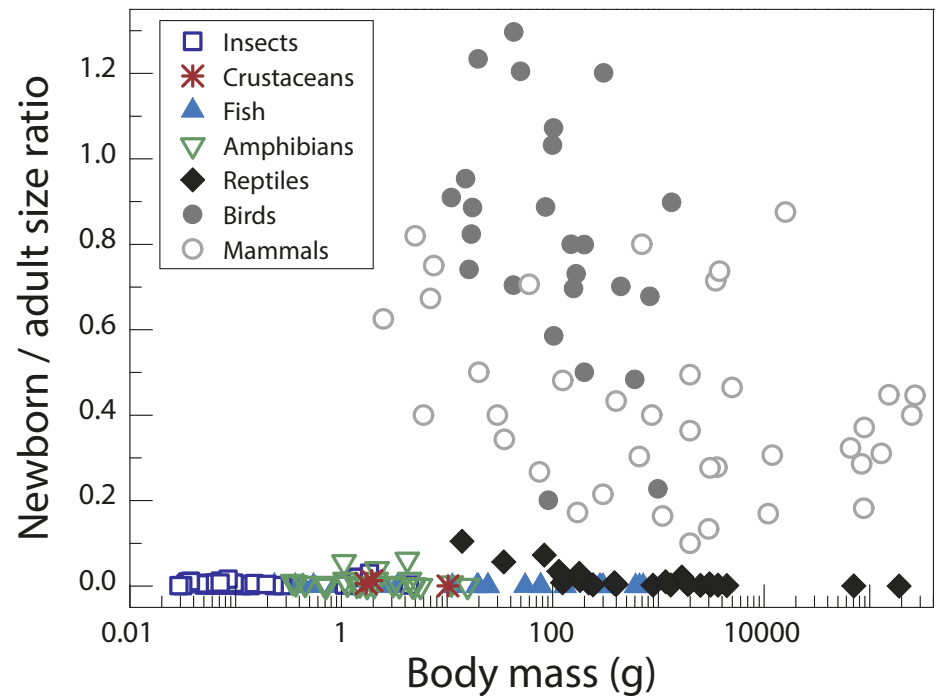
# The simplest, fully size-structured analogue

- Juveniles grow in body size, adults only reproduce

- Ingestion, maintenance, somatic growth and reproduction ***proportional to body size***

- Mortality ***constant within each stage***

- Bio-energetics model: ***mass conservation***

**Juveniles and adults may differ in:**
- **Mass-specific** growth and reproduction (net-production rate of new biomass)      $\nu_J(R), \quad \nu_A(R)$

- Mortality:      $\mu_J, \quad \mu_A$

# The size-structured population model
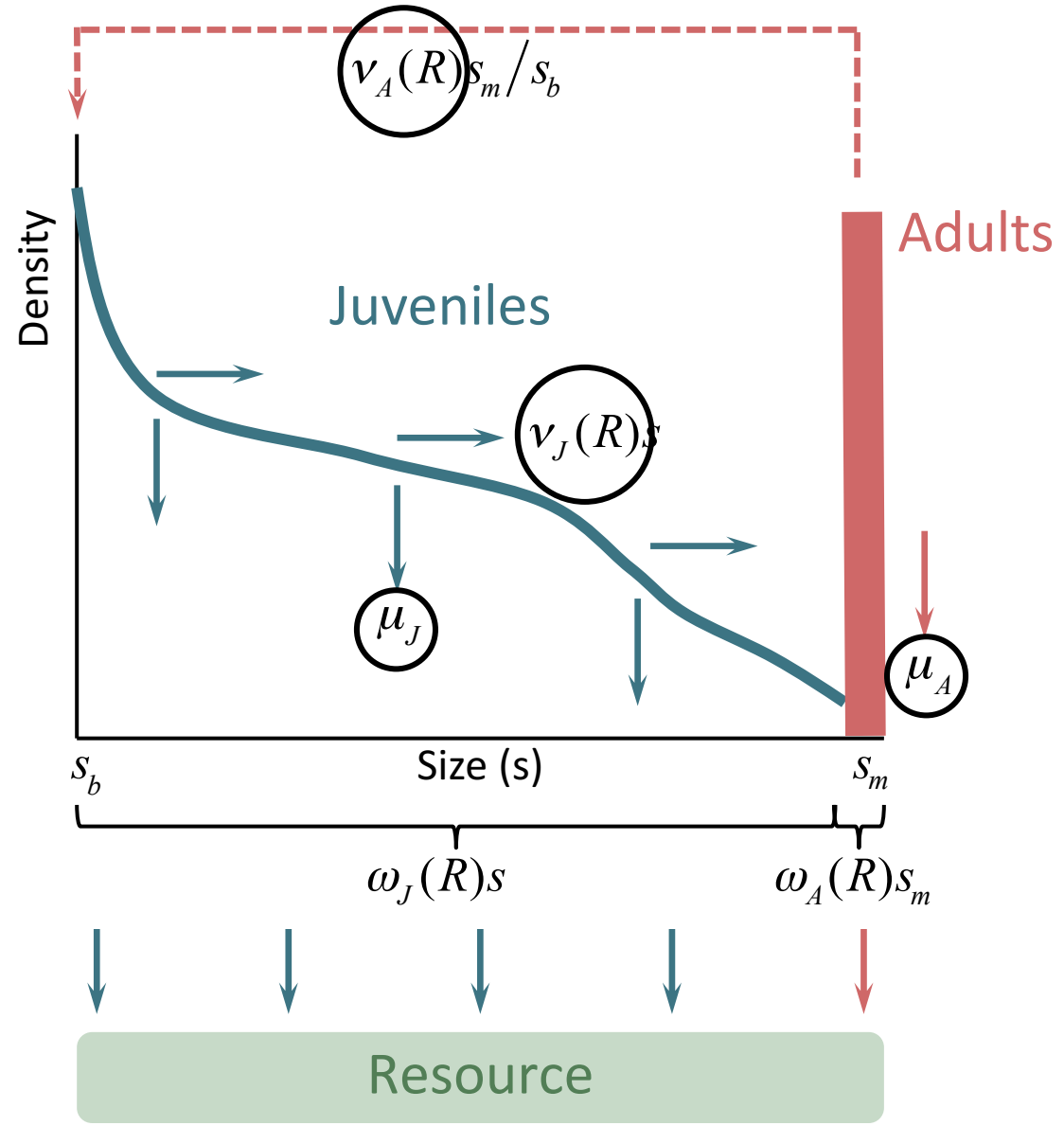
# The size-structured population model

$$\frac{\partial c(t,s)}{\partial t} + \nu_J(R)\frac{\partial(sc(t,s))}{\partial s} = -\mu_J c(t,s) \qquad \text{for } s_b \le s < s_m$$

$$\nu_J(R)s_b\, c(t,s_b) = \frac{\nu_A(R)s_m}{s_b}\, C_A(t)$$

$$\frac{dC_A}{dt} = \nu_J(R)s_m\, c(t,s_m) - \mu_A\, C_A(t)$$

$$\frac{dR}{dt} = \rho(R_{max} - R) - \omega_J(R)\int_{s_b}^{s_m} sc(t,s)ds - \omega_A(R)s_m C_A(t)$$
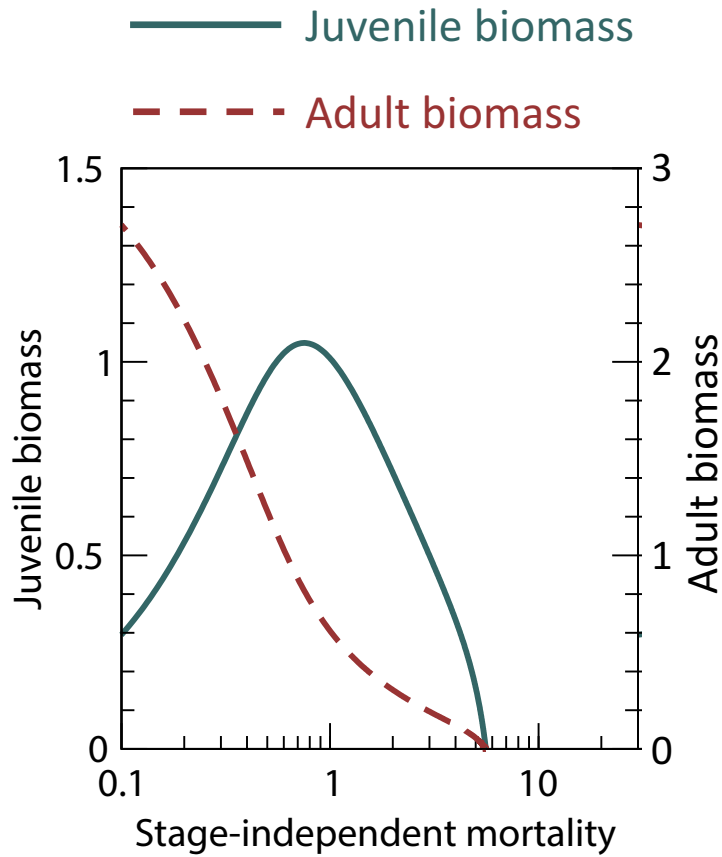
Mass conservation:
Juvenile growth and adult reproduction proportional to body size:

$$g(s,R) \;=\; \nu_J(R)s \;=\; (\sigma\omega_J(R) - T)\,s$$

$$b(s_m,R) \;=\; \frac{\nu_A(R)s_m}{s_b} \;=\; \frac{(\sigma\omega_A(R) - T)\,s_m}{s_b}$$
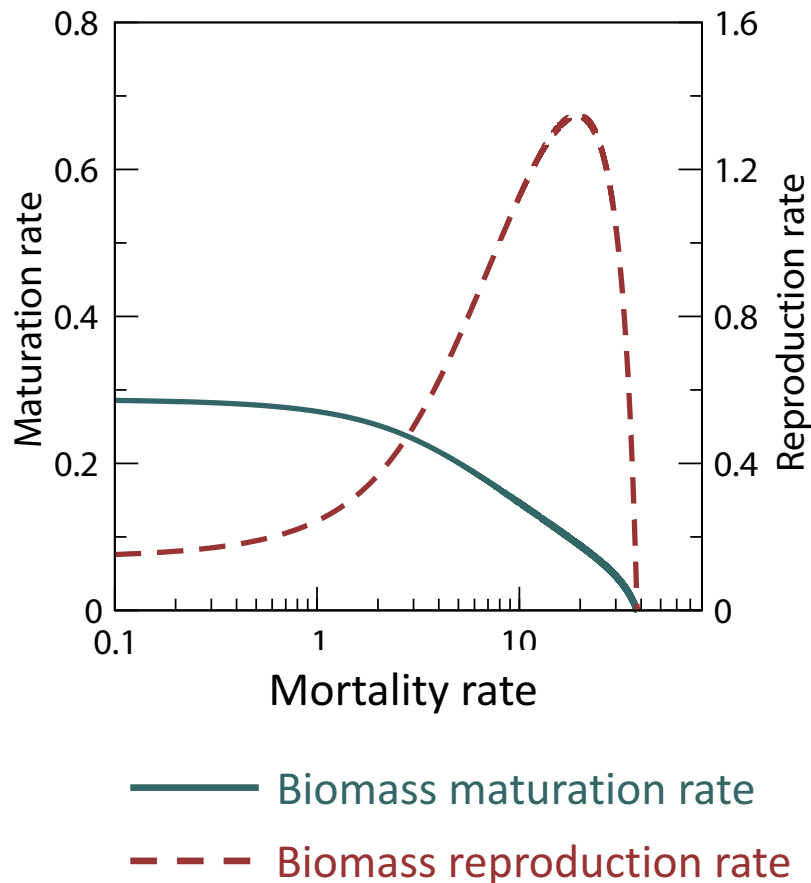
# Equilibrium changes with increasing mortality



**Reproduction control:** $\nu_J(\tilde{R}) > \nu_A(\tilde{R}) > 0$

# Asymmetric changes in reproduction and maturation with increasing mortality



Biomass maturation rate
Biomass reproduction rate

**When adults compete more:**

- Low adult fecundity, high juvenile survival

- Adults dominate

- *Adults use most of their intake for maintenance* (no production)

- Mortality releases adult competition, increases reproduction and juvenile biomass
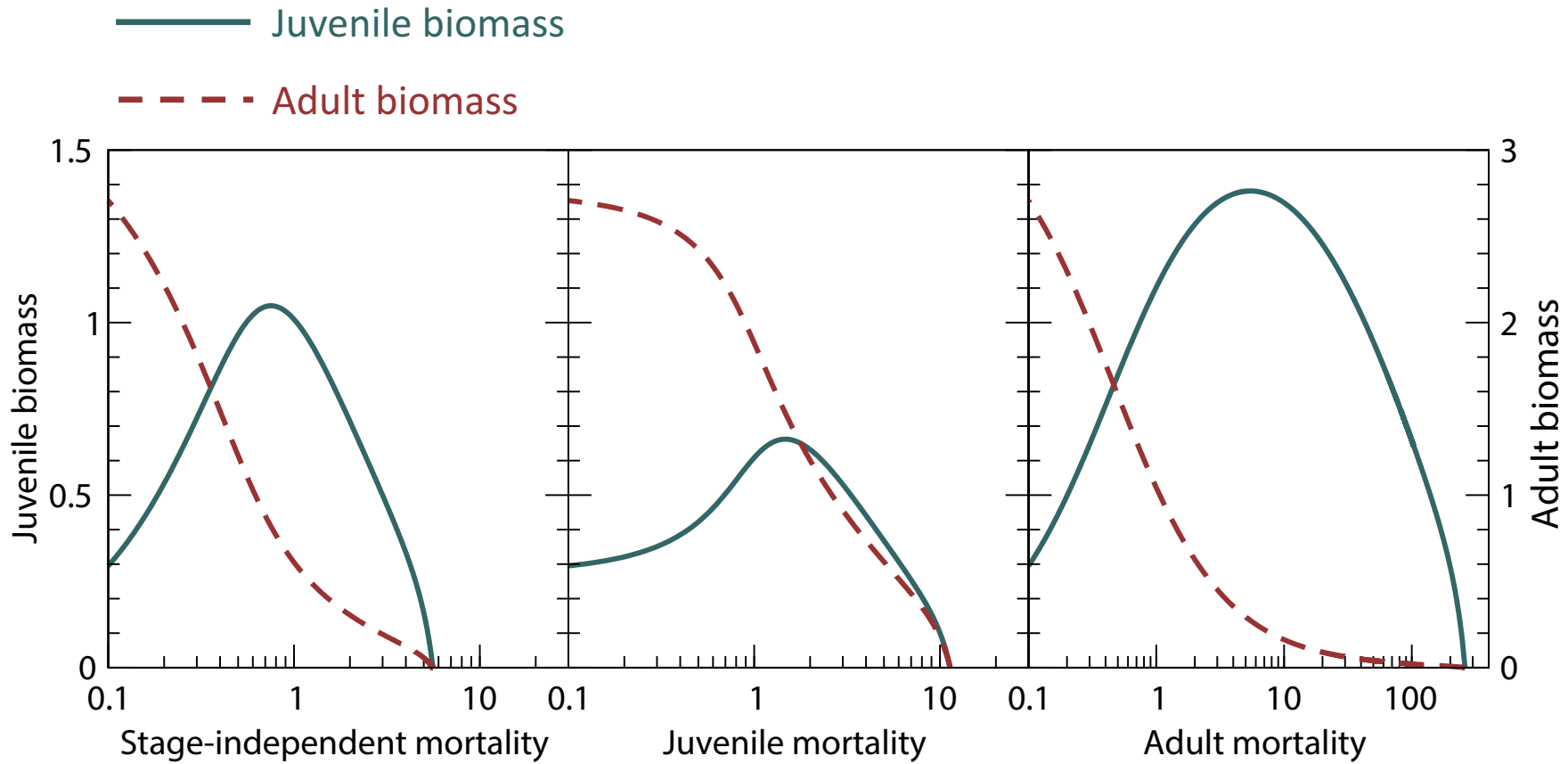
# Interplay between maintenance and mortality
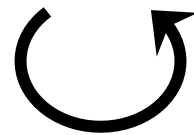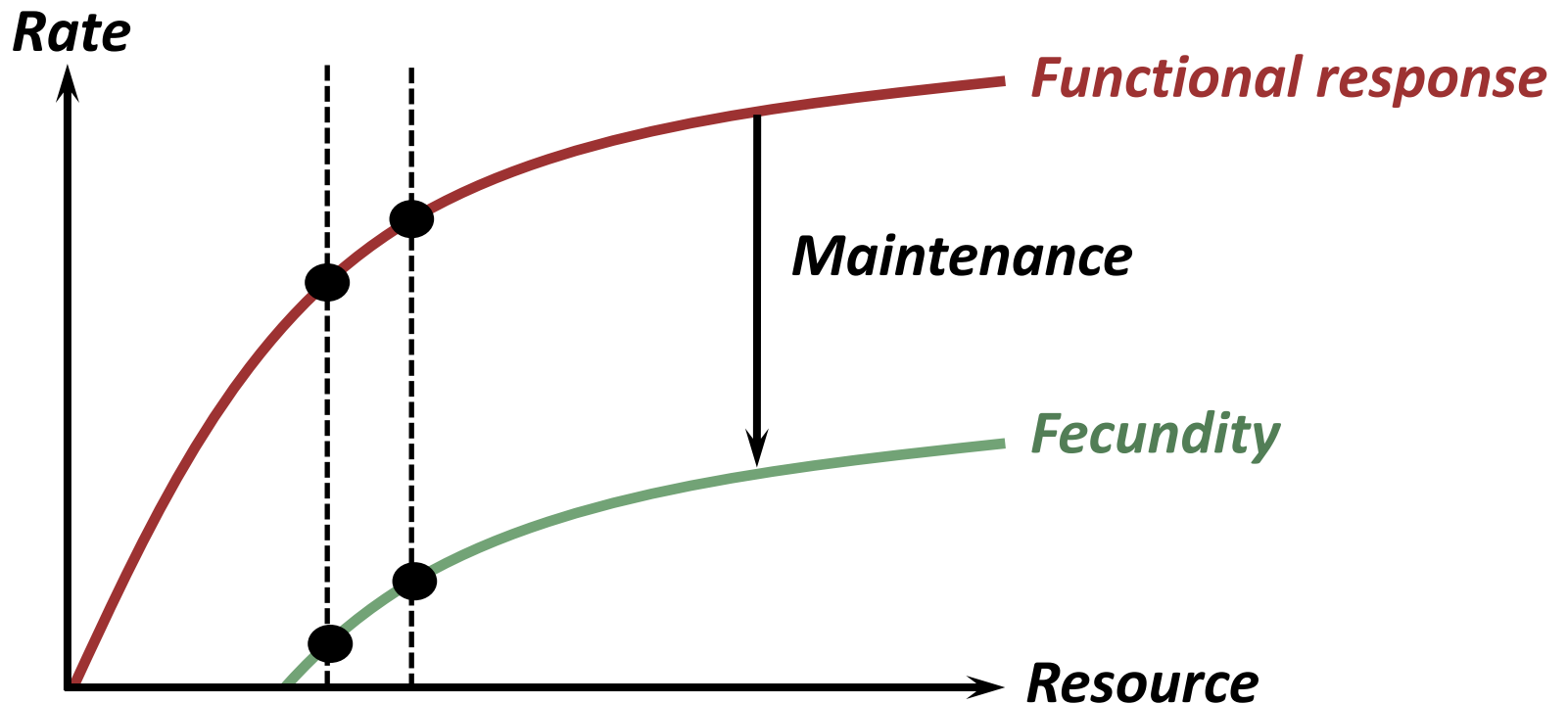


**20% decrease** in density increases ingestion by roughly 20%, but **doubles** adult fecundity
$\Rightarrow$ **60% increase in total reproduction**

**Mortality decreases maintenance losses and increases production efficiency**

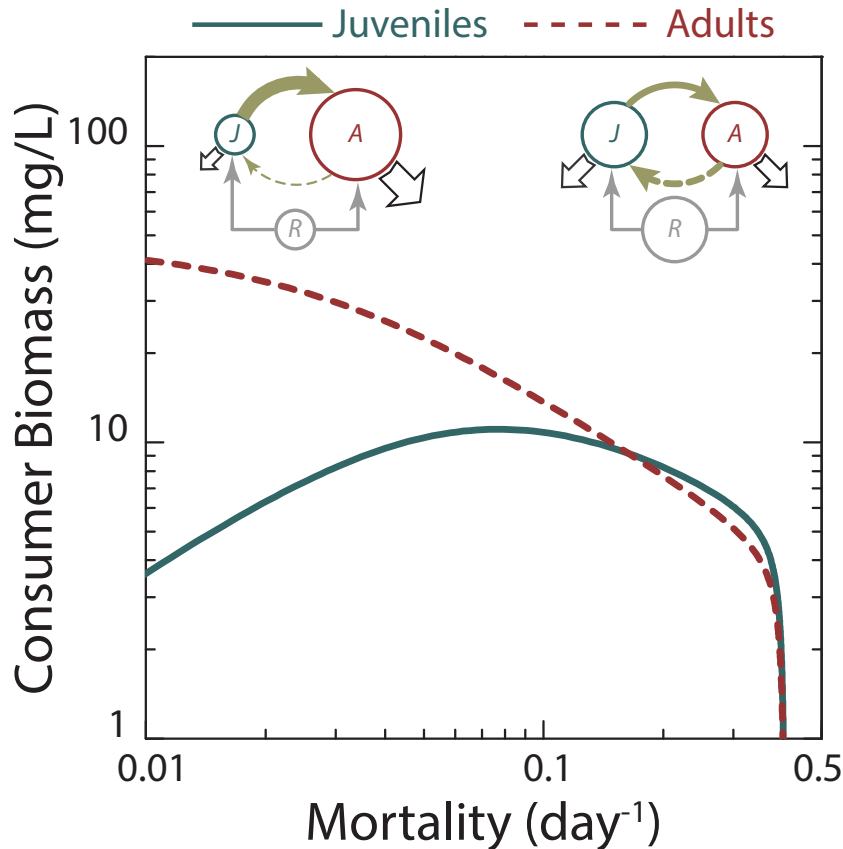# Equilibrium changes with increasing mortality



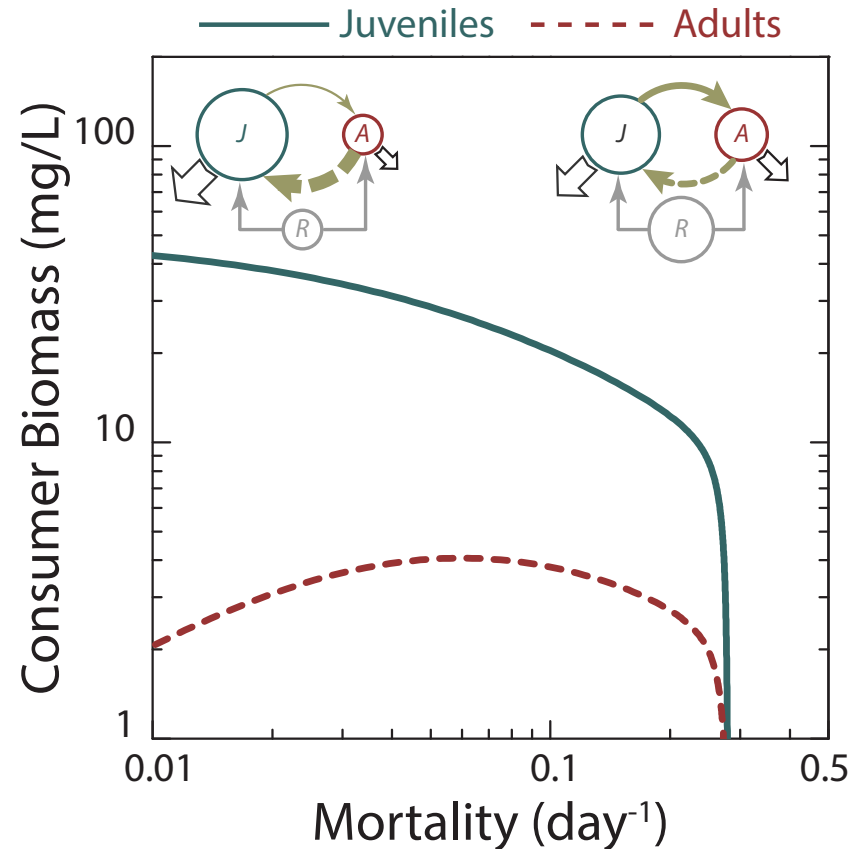**Reproduction control:** $\nu_J(\tilde{R}) > \nu_A(\tilde{R}) > 0$

# Ontogenetic asymmetry

$$\nu_J(\tilde{R}) > \nu_A(\tilde{R}) > 0$$

$$\nu_A(\tilde{R}) > \nu_J(\tilde{R}) > 0$$



**Reproduction control**
**Mortality increases**
**juvenile biomass**

**Development control**
**Mortality increases**
**adult biomass**