Daphnia revisited: an example of local stability and bifurcation analyses for physiologically structured population models

NDNS+ workshop
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@Eindhoven TU
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Based on the paper
Odo Diekmann, Mats Gyllenberg, Hans Metz, SN, Andre de Roos
Daphnia revisited: local stability and bifurcation theory for physiologically structured population models explained by way of an example.
Journal of Mathematical Biology *in press*.

Delay equations

- A couple system of renewal and delay differential equation

Space

$$X := L^1\left([-h,0];\mathbb{R}\right), \quad Y := C\left(([-h,0];\mathbb{R}\right).$$

Initial condition

$$(\varphi,\psi) \in X \times Y, \quad b(t) = \varphi(t) \text{ and } S(t) = \psi(t), \quad -h \le t \le 0$$

A general form for a finite delay case

$$\begin{cases} b(t) = F_1(b_t, S_t), \\ \dfrac{dS}{dt}(t) = F_2(b_t, S_t) \end{cases}$$

where $S_t(\sigma)\colon\ \sigma \mapsto S(t+\sigma), \quad \sigma \le 0$

Mathematical theory

O. Diekmann *et al*, Delay equations: functional, complex, and nonlinear analysis, Springer, 1995

☑ A finite delay case

O. Diekmann *et al*, Stability and bifurcation analysis of Volterra functional equations in the light of suns and stars, SIAM J. Math. Anal. 39: 1023--1069, 2007

☑ An infinite delay case

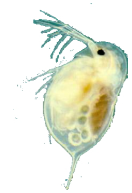
O. Diekmann *et al*, Abstract delay equations inspired by population dynmics, in Functional analysis and evolution equations. 187--200, 2008

O. Diekmann *et al*, Equations in infinite delay, submitted.

Resource-consumer system

$S(t)$: food (algae) concentration (resource)

$b(t)$: *Daphnia* population birth rate (consumer)



$$b(t) = \int_0^\infty b(t-a)\beta(\Xi(a;S_t), S(t))\mathcal{F}(a;S_t)da,$$

$$\frac{dS}{dt}(t) = f(S(t)) - \int_0^\infty b(t-a)\gamma(\Xi(a;S_t), S(t))\mathcal{F}(a;S_t)da.$$

$\Xi(a;S_t)$: The current body size of an individual with age a

$\beta(\Xi(a;S_t), S(t))$: the probability per unit of time of giving birth

$\gamma(\Xi(a;S_t), S(t))$: the rate of food consumption of an individual

$\mathcal{F}(a;S_t)$: the survival probability of an individual

Model ingredients

☑ Individual body size growth and survival

An individual has age *a* at the current time *t*

$\Xi(a; S_t)$: The current body size of an individual with age a

$$\begin{cases} \dfrac{d\xi}{d\tau}(\tau) = g(\xi(\tau), \psi(-a+\tau)), \quad \xi(0) = \xi_b. \\ \Xi(a;\psi) := \xi(a; a, \psi) \end{cases}$$

$\mathcal{F}(a; S_t)$: the survival probability of an individual

$$\begin{cases} \dfrac{d\mathcal{G}}{d\tau}(\tau) = -\mu(\xi(\tau; a, \psi), \psi(-a+\tau))\mathcal{G}(\tau),\ \mathcal{G}(0) = 1 \\ \mathcal{F}(a;\psi) = \mathcal{G}(a; a, \psi) \end{cases}$$

Linearised stability

- Steady state $(\bar{b}, \bar{S})$

R_0: the basic reproduction number of the *Daphnia*

$$R_0(\overline{S}) = \int_0^\infty \beta(\Xi(a;\overline{S}),\overline{S})\mathcal{F}(a;\overline{S})da$$

A steady *Daphnia* population

$$R_0(\overline{S}) = 1$$

$$\bar{b} = f(\overline{S}) / \int_0^\infty \gamma(\Xi(a;\overline{S}),\overline{S})\mathcal{F}(a;\overline{S})da$$

We can derive steady state age-size relation and survival probability (not shown)

Linearised stability

- Linearised system

$$\begin{cases} y(t) = & c_1 z(t) + \int_0^\infty (k_{11}(a) y(t-a) + k_{12}(a) z(t-a)) da, \\ \frac{dz}{dt}(t) = & c_2 z(t) + \int_0^\infty (k_{21}(a) y(t-a) + k_{22}(a) z(t-a)) da \end{cases}$$

- Characteristic equation

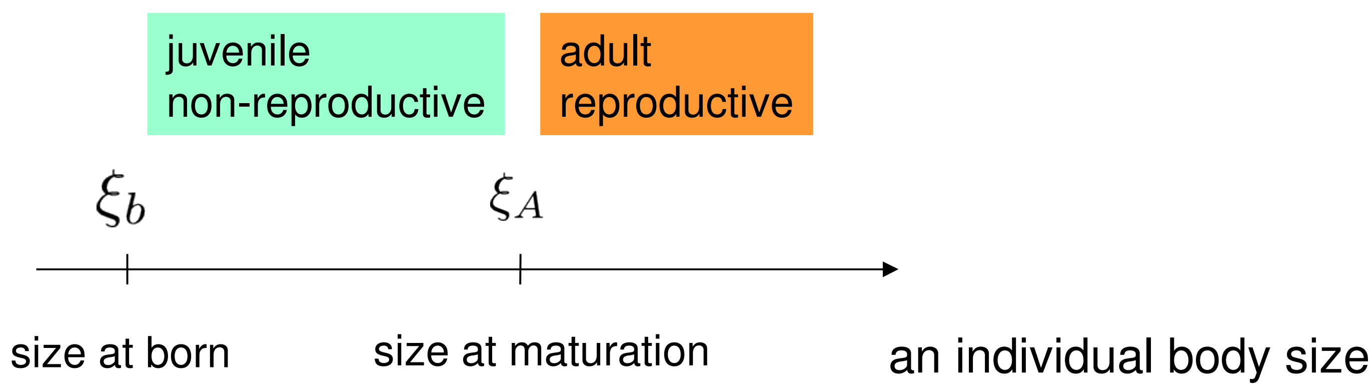
$$\left(1 - \widehat{k}_{11}(\lambda)\right)\left(\lambda - c_2 - \widehat{k}_{22}(\lambda)\right) = \widehat{k}_{21}(\lambda)\left(c_1 + \widehat{k}_{12}(\lambda)\right)$$

where $\widehat{k}_{ij}(\lambda) := \int_0^\infty e^{-\lambda a} k_{ij}(a) da$

A special case: stage structure

- Stage transition from juvenile to adult

Maturation



$\bar{a} = \bar{a}(\psi)$: the age of the individuals that mature exactly now

$$b(t) = \int_{\bar{a}(S_t)}^{\infty} b(t-a)\beta(\Xi(a;S_t), S(t))\mathcal{F}(a;S_t)da.$$

A special case: stage structure

C.f., De Roos et al, Theor. Pop. Biol. 2003

☑ Variable maturation delay

Assumption

Model ingredients g, μ, β and γ are indipendent of ξ

$$\int_{-\tau}^{0} g(S_t(\theta))d\theta = \xi_A - \xi_b$$

variable maturation delay

$$\tau = \tau_m(S_t)$$

time

ξ_b juvenile ξ_A adult

an individual body size

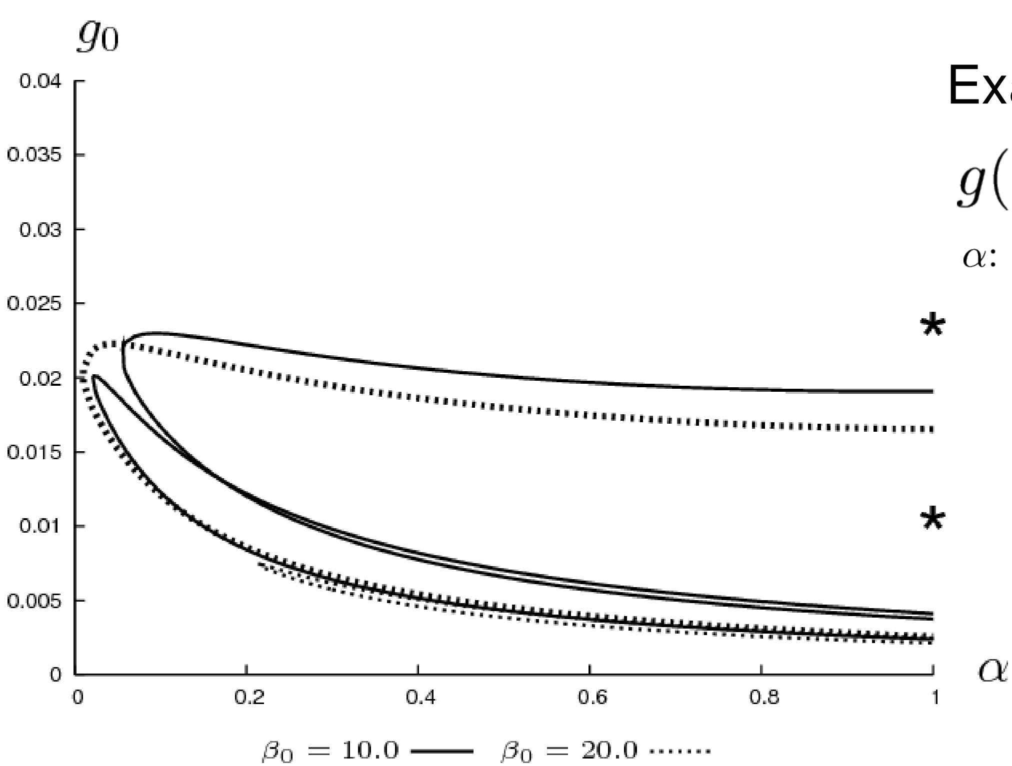
size at born size at maturation

Numerical bifurcation analysis

Hopf bifurcation and population cycles

Characteristic equation: $P(\lambda; a, b) = 0 \quad a,\, b \in \mathbb{R}$

$\lambda = i\omega$: a parametrized curve $(a(\omega), b(\omega))$



Example:

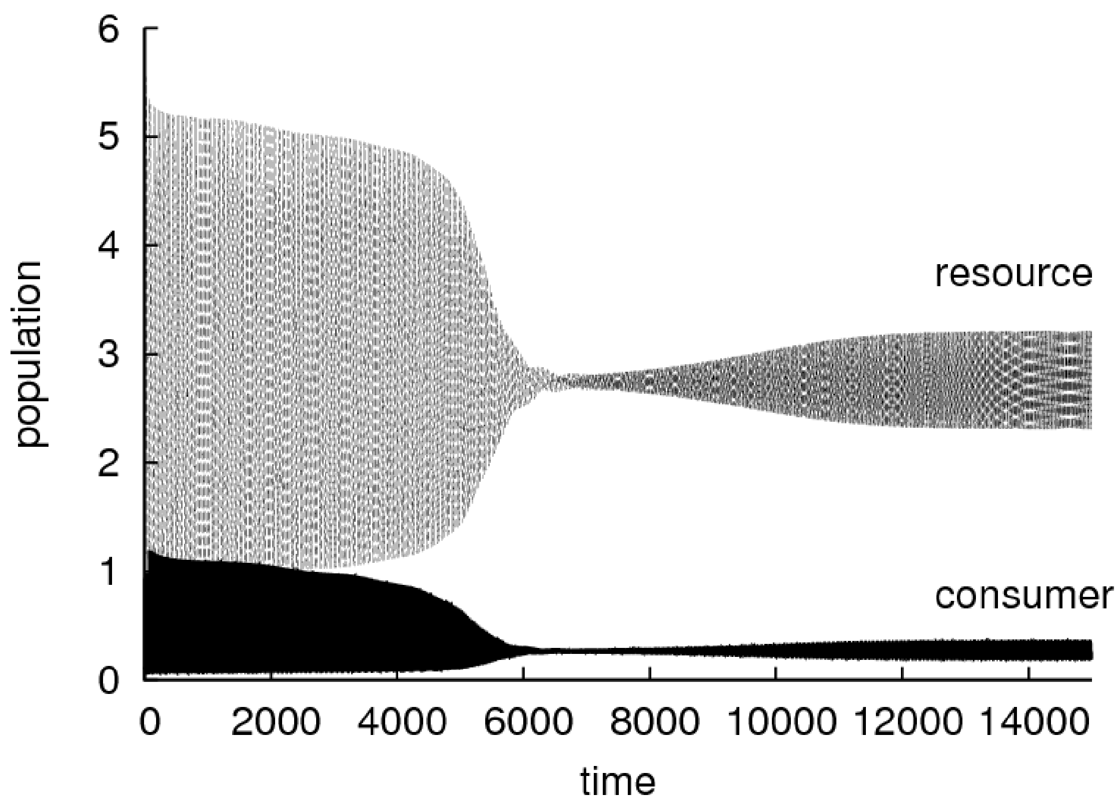
$$g(S) = g_0((1-\alpha)A + \alpha S)$$

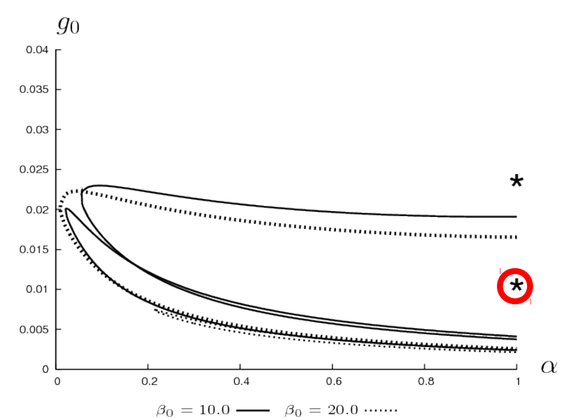
α: A fraction of juveniles to exploit S

C.f., Diekmann Springer 1995

Numerical simulation

- ☑ By Escalator Boxcar Train method De Roos et al, Am Nat 1992





Future work

- Numerical analysis

  De Roos et al, Bull. Math. Biol. 2009

  Numerical equilibrium analysis for structured consume-resource models

  Future work: numerical continuation of periodic orbits etc...

- Another direction

  Application of the theory of physiologically structured population models and delay equations TO

  epidemiological model, cell biological context etc...