The Circulator, a Hybrid Discrete-Continuous Time Model for Size-Structured Semelparity

Sebastiaan Janssens

Mathematical Institute

Utrecht University

Workshop Nonlinear Dynamics of Natural Systems+

Eindhoven University of Technology

April 14, 2010

Outline

1. A Caricatural Model for Size-Structured Semelparity
2. Single-Cohort Solutions. The Finite-Dimensional Case
3. Towards a Treatment in the Space of Measures

Outline

1. A Caricatural Model for Size-Structured Semelparity
2. Single-Cohort Solutions. The Finite-Dimensional Case
3. Towards a Treatment in the Space of Measures

What is a Structured Population Model?

Structured Population Model

A model for a (biological) population is called structured when its constituent individuals are distinguished on the basis of one or more physiological attributes, such as age or size.

- **I**ndividual state: The current age or size of an individual
- Interaction is indirect: Individuals affect and are affected by the environment
- **P**opulation state: Distribution over all possible individual states
- We choose to neglect spatial dependence

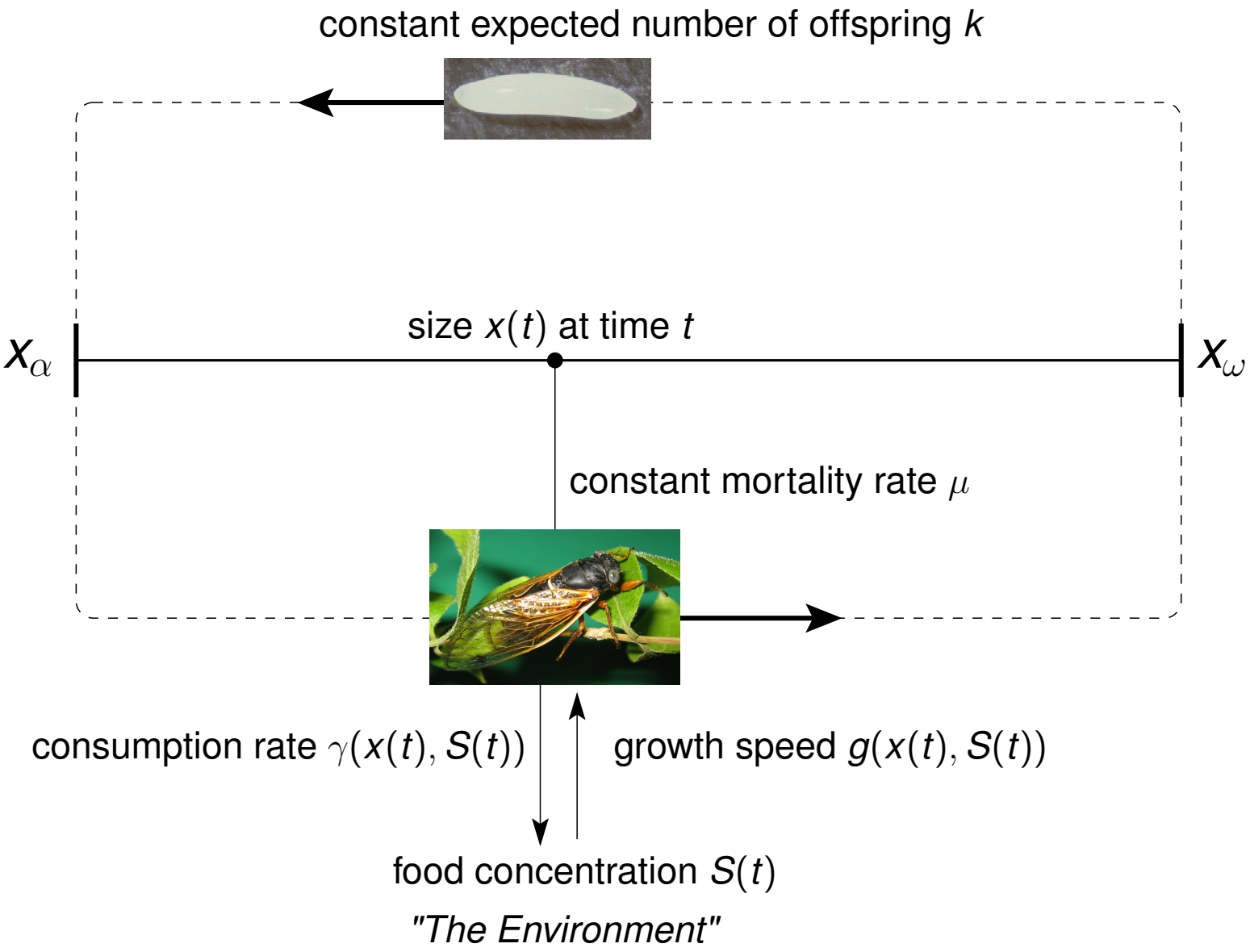
Semelparity

Size or Age Structured Semelparity

Individuals reproduce only once, upon reaching a fixed maximum age or size, and die thereafter.

- Age-structured semelparity
  Examples: Pacific salmon, cicadas, annual and biennial plants
- Size-structure may predominate over age-structure
  Examples: Certain biennial and perennial plants
- See the study by Werner and Caswell, 1977, *Ecology* **58** on teasel (*Dipsacus sylvestris*, Dutch: Kaardebol)

The Model. Individual Life Cycle



The Model. Evolution of the Population State.

- Initial conditions: Food level $S_0 \in \mathbf{R}_+$ and distribution $m_0 \in \mathcal{M}_+[x_\alpha, x_\omega] \equiv \mathcal{M}_+$ over all possible sizes
- Key assumption: The growth speed $g(x(t), S(t))$ is bounded away from zero (can be relaxed)
- Consequence 1: For each initial condition (m_0, S_0) there exists a time $T(m_0, S_0)$ at which a (possibly imaginary) cohort of initial size x_α has reached reproductive size x_ω
- Consequence 2: There exists an invertible interval map

$$r(\cdot, m_0, S_0) : [x_\alpha, x_\omega] \to [x_\alpha, x_\omega]$$

that assigns to a cohort of initial size x_0 *its* size after a full circle, at time $T(m_0, S_0)$

The Model. Evolution of the Population State.

The Circulator Mapping

The foregoing leads us to define a mapping F of $\mathcal{M}_+ \times \mathbf{R}_+$ by

$$F(m_0, S_0) = \begin{bmatrix} ke^{-\mu\, T(m_0, S_0)}\, m \circ r^{-1}(\cdot, m_0, S_0) \\ S(T(m_0, S_0), m_0, S_0) \end{bmatrix}$$

- First component tells how initial measure m_0 is distorted by the interval map $r(\cdot, m_0, S_0)$
- Second component is food level after population has gone full circle

Invariance of L^1 and $\sum_{i=1}^{N} \alpha_i \delta_{x_i}$

- When initial measure $m_0 \in L^1$ we are in a limiting case of

  Diekmann, Gyllenberg, Metz, Nakaoka, De Roos
  Daphnia revisited: local stability and bifurcation theory for physiologically structured population models explained by way of an example
  J. Math. Biol., published online September 22, 2009.

- When m_0 is a finite linear combination of Dirac measures,

  Waltraud Huyer
  On periodic cohort solutions of a size-structured population model
  J. Math. Biol., 35, 1997.

Outline

1. A Caricatural Model for Size-Structured Semelparity
2. Single-Cohort Solutions. The Finite-Dimensional Case
3. Towards a Treatment in the Space of Measures

Huyer's Special Case: Finitely Many Cohorts Present

- Initial sizes $x_\alpha, x_{2,0}, \ldots, x_{n,0} \in [x_\alpha, x_\omega]$
- Initial amplitudes $N_{1,0}, \ldots, N_{n,0} \in \mathbf{R}_+$
- Initial food level $S_0 \in \mathbf{R}_+$

Circulator-map induces map F_n on $\mathbf{R}_+^{2n}$ defined through solution of ODE modelling growth, survival and consumption

$$\begin{cases} \dfrac{dx_i}{dt}(t) = g(x_i(t), S(t)) & i = 1, \ldots, n \\ \dfrac{dN_i}{dt}(t) = -\mu\, N_i(t) & i = 1, \ldots, n \\ \dfrac{dS}{dt}(t) = h(S(t), \beta) - \displaystyle\sum_{i=1}^{n} \gamma(x_i(t), S(t))\, N_i(t) & \end{cases}$$

plus reproductive jumps at times t for which $x_n(t) = x_\omega$

Huyer's Special Case (Cont'd)

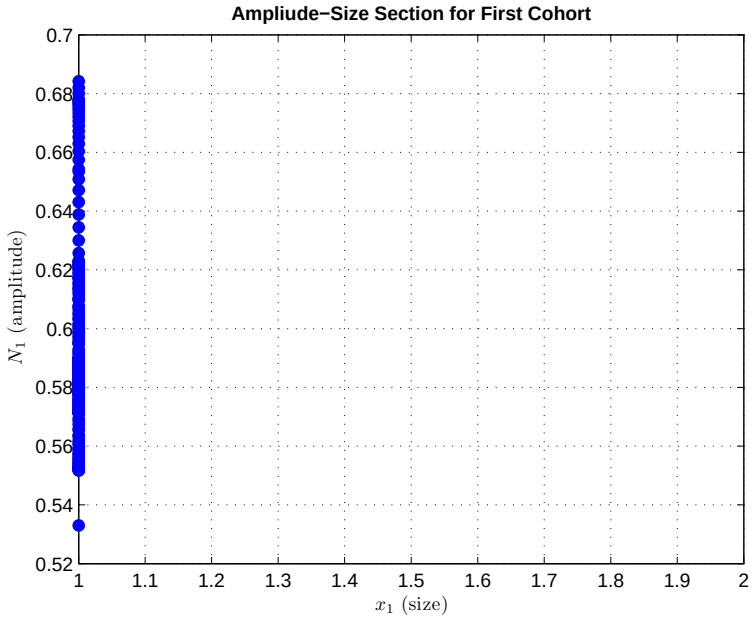
- F_n conserves ratios $\frac{N_{0,i}}{N_{0,j}}$ between cohort amplitudes
- Each initial condition selects a hyperplane in $\mathbf{R}^{2n}$ of codimension $n-1$
- Intrinsic food level too low ($\beta < \beta_c$) $\Rightarrow$ extinction
- For $\beta > \beta_c$ at least two scenarios are possible:

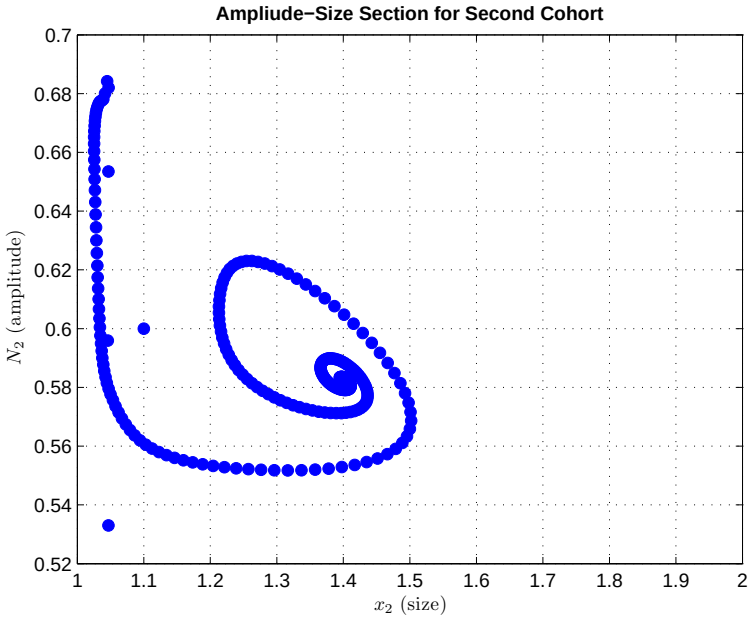
(1) There exists a (locally) stable fixed point of F_n in $x = x_\alpha$ with no other cohorts present

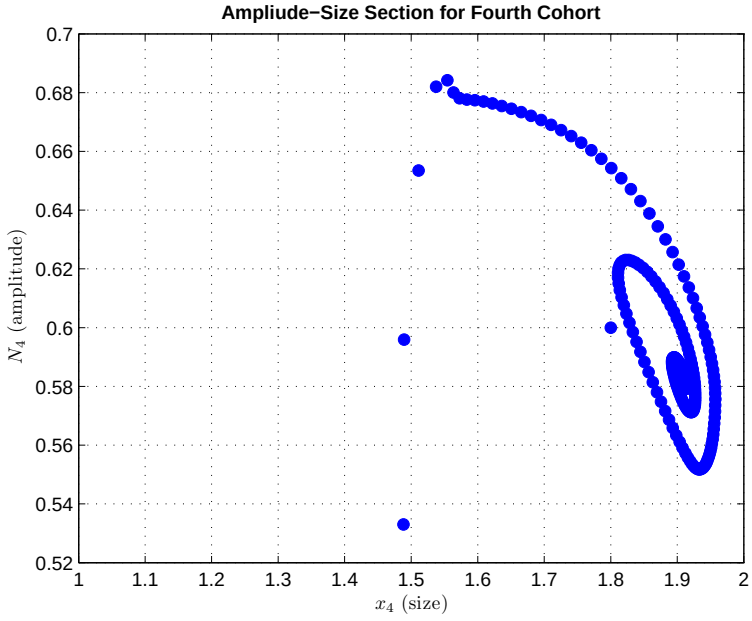
(2) The fixed point in x_α exists, but is unstable. In addition, there exists a stable multiple-cohort fixed point of F_n

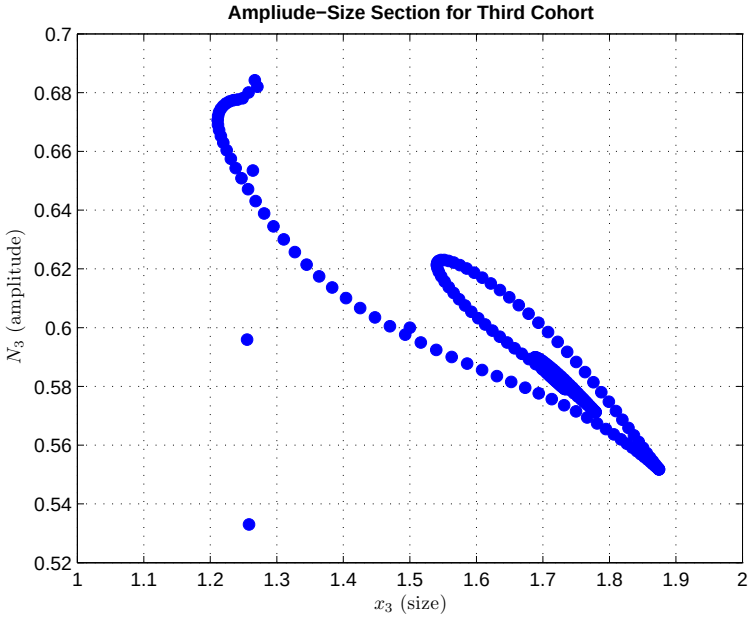
We discuss an example of (2)

Huyer's Special Case: Multiple-Cohort Fixed Point









Outline

1. A Caricatural Model for Size-Structured Semelparity
2. Single-Cohort Solutions. The Finite-Dimensional Case
3. Towards a Treatment in the Space of Measures

Aims, Problems and Progress

Recall the circulator operator on $\mathcal{M}_+ \times \mathbf{R}_+$,

$$F(m_0, S_0) = \begin{bmatrix} ke^{-\mu\, T(m_0,S_0)}\, m \circ r^{-1}(\cdot, m_0, S_0) \\ S(T(m_0, S_0), m_0, S_0) \end{bmatrix}$$

We want to do local stability and bifurcation analysis, à la Huyer but now in $\mathcal{M}_+ \times \mathbf{R}_+$

- We topologize $\mathcal{M}$ by the weak*-topology
- On $\mathcal{M}_+$ this topology is normizable by the Kantorovich - Rubinshtein (-Dudley - Hutchinson...) norm, which coincides with the dual norm of the space BL(X) of bounded Lipschitz functions

However, we will not use this norm. Instead we work with the dual norm of the space $C^\ell[x_\alpha, x_\omega]$ of ℓ-times differentiable functions

Aims, Problems and Progress (Cont'd)

The reason: Our test functions are C^ℓ-smooth instead of merely Lipschitz continuous, while all other important properties are conserved.

Example

The derivative of F in a point of the form (δ_x, S_0) involves the functional $\phi \mapsto -\phi'(x)$. This functional is defined on $C^\ell[x_\alpha, x_\omega]$ but not on $\mathrm{BL}(X)$.

Why we do not work within the space of distributions:

- This is not a normed space. (Not even a Fréchet-space in the sense of Rudin)
- There does not exist a canonical theory of differentiation and spectral analysis in spaces without norm
- In particular we cannot hope for Desch-Schappacher type linearization estimates

Outlook

- Spectral analysis of linearization of F at fixed points of Dirac type $\Rightarrow$ Principle of Linearized (In)stability
- Generalization of Huyer's stability criterium to the measure setting
- Study destabilization of single-cohorts both in finite and infinite dimensions. What kind of dynamics is possible?

This work is done together with

Odo Diekmann (UU) Universiteit Utrecht

Stephan van Gils (UT, UU) UNIVERSITEIT TWENTE.