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Spectral properties of a semi-discretized McKendrick equation

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Abstract

In this paper, we perform a numerical study on the eigenvalues of the operator of a semi-discretized age-structured predator-prey model. The age-structuration is based on an agile modeling framework for population dynamics. We also prove a theoretical result on the distribution of the eigenvalues of a semi-discretized McKendrick equation. We show that, under regularity assumptions, and after a rescaling step, the eigenvalues converge to the unit circle as the number of age groups goes to infinity. A sufficient condition to get this convergence consists in having piecewise-constant birth and death rates; by using random values of birth and death rates, we also show numerically that having not enough regular values invalidates the result. We complete this study with properties on the original McKendrick equation, such as the compactness of its operator, the countability of its spectrum, and the fact that the eigenvectors form a complete basis of the function space.

Keywords: population dynamics, McKendrick equation, predator-prey model, spectral problems, linear stability

MCS Classification: 92D25 , 92-10 , 34D20 , 34M46 , 35P20

Introduction

The McKendrick equation and the predator-prey model are well known population dynamics models. The McKendrick-von Foerster equation first appeared in articles dealing with epidemiological and disease modeling, but dealt with demographic modeling (McKendrick, 1925; Kermack and McKendrick, 1927).

This equation is classically written

$$\partial_t \phi(t, a) + \partial_a \phi(t, a) + \mu(a) \phi(t, a) = 0,$$

where ϕ is the population density, a the age and μ the mortality rate, and completed with a boundary condition

$$\phi(t, 0) = \int_0^{+\infty} b(a) \phi(t, a) da,$$

where b is the natality rate, and an initial condition

$$\phi(0, a) = \phi_0(a).$$

b is usually zero out of a fertility interval $[a_0, a_1]$, with $0 < a_0 < a_1$.

The McKendrick equation constitutes an important tool in demography, and is often rediscovered by mathematicians studying nonlinear population dynamics problems (Hoppenstaedt, 1975; Webb, 1985).

Several approaches exist to study structured population dynamics. Among them, let us cite integral formulation (Sharpe and Lotka, 1911), difference equations (Thompson, 1931; Cole, 1954), partial differential equations (McKendrick, 1925; von Foerster, 1959) and projection matrix (Cannan, 1895; Leslie, 1945). On the fundamental PDE approach, some preliminary observations have been carried on the spectrum of the operator involved in the integral formulation. As a compact operator, it has a countable spectrum, and one can express the solution as a superposition of eigenfunctions. In Keyfitz and Keyfitz (1997), authors compare the McKendrick PDE to the above-mentioned approaches and derive solutions under suitable hypotheses.

More recently, the introduction of nonlinear models breathed new life into age-structured populations study. In Gurtin and Maccamy (1974), using nonlinear integral Volterra equations, authors showed the existence, uniqueness and convergence to an equilibrium of solutions of a nonlinear Sharpe-Lotka-McKendrick model. This work paved the way to breakthroughs on nonlinear models, as much on theoretical developments as on biological applications (see Iannelli (1995) for an exhaustive approach). The growing mathematical complexity of nonlinearities in age-structured models led to developments of new tools and methods, such as linear and nonlinear operator semigroups in Banach spaces, with a functional analysis approach (Diekmann and Getto, 2005).

When a population’s description goes beyond the assumptions of [Keyfitz and Keyfitz \(1997\)](#), it is often necessary to introduce new methods for modeling and analyzing such complex structured population models. For a complete view on structured populations, we refer to [Perthame \(2007\)](#). We also mention the works of [Diekmann et al. \(1994, 1998\)](#) for an approach of structured population dynamics models which presents similarities with the method we develop, presented below.

At Dassault Systèmes, we designed an agile modeling framework and developed a model generator, able to generate simulatable models conforming to assumptions and population structure given as input¹.

The framework’s formalism is an extension of the McKendrick equation, where the mortality term $\mu(a)\phi(t, a)$ is replaced with generic exchanges terms, such as

$$\int_{\mathbb{D}} \kappa(t, \phi(t), a, x, y) \phi(t, a, y) \, dy,$$

where x (resp. y) represents the origin (resp. destination) state, which belongs to the state domain \mathbb{D} .

A conservative form of exchange terms, written as

$$\int_{\mathbb{D}} (k(t, \phi(t), a, x, y) \phi(t, a, y) - k(t, \phi(t), a, y, x) \phi(t, a, x)) \, dy,$$

is also studied, to model exchanges between the compartments of our structured and generic population.

To simulate structured models, we operate a semi-discretization on the age derivative, and get a dynamical system of ODE simulatable by Dassault Systèmes’s solvers embedded in the Dymola Software ([Brück et al., 2002](#)). The input format of Dymola being models written in the Modelica language ([Fritzson and Engelson, 1998](#)), the modeler generates Modelica files by coupling an object-oriented implementation of the structured population formalism with a templating approach, using the Python library Jinja2 ([Ronacher, 2014](#)).

In our previous work, we applied this framework to the simulation of a structured predator-prey model, exploring various and interesting phenomena in terms of asymptotic behaviors. The issue of such population system’s stability comes naturally in the discussion, wondering under which assumptions a population system converges to a fixed point, or ends up with a cyclic trajectory, or even presents a chaotic evolution.

The issue of stability and asymptotic behavior is one of the most common when dealing with the analysis of dynamical systems of ODEs. Linear stability refers to the ability of a system to come back to an equilibrium point when it undergoes small perturbations ([Magiros, 1966](#)). The usual approach consists in writing the jacobian matrix of the differential system and examining its eigenvalues. The sign of the real

¹see our unpublished work *An agile framework for population dynamics* available at <https://hal.science/hal-04646788>

parts of eigenvalues gives insight on the equilibrium point's nature. See [Bellman \(1953\)](#); [LaSalle \(1976\)](#); [Demailly \(2006\)](#) for further perspectives on linear and nonlinear stability analysis. Beyond linear and local stability, many definitions of stability for dynamical systems have been given, such as the stability in the sens of Lyapunov ([Lyapunov, 1992](#)), Poincaré ([Magiros, 1985, 1965](#)) or Lagrange ([Gyftopoulos, 1963](#); [Bhatia and Szegö, 1970](#)). Lyapunov's method addresses stability problems both near and far from the equilibrium. It consists in finding a positive definite function, called a Lyapunov function, whose derivative's sign will give insight on the equilibrium point asymptotic stability. To go further into nonlinear stability analysis and Lyapunov method, see [Bhatia and Szegö \(1970\)](#); [Roussel \(2019\)](#). We also cite [Arnol'd \(1992\)](#) as an exhaustive reference on ordinary differential equations.

To tackle this issue of stability and asymptotic behavior, we got interested in computing the eigenvalues of classic demographic models. We observed that the eigenvalues are distributed in circular structures. Our goal is to better understand these structures. The fact that these structures appear even in a very simple problem such as the semi-discretized McKendrick equation support the intuition that they are due to the discretization process.

This article is divided in three sections. In [section 1](#), we derive from the well-known predator-prey model an age-structured, semi-discretized formulation, and carry numerical observations on the distribution of jacobian's eigenvalues at equilibrium points.

In [section 2](#), we study the simpler McKendrick-von Foerster equation, semi-discretized in age, and prove a theoretical result on the distribution of the system's eigenvalues. We show that, in some sense, and under some regularity assumptions, the set of eigenvalues is dense into the unit circle of the complex plane. We then discuss the role of the regularity assumptions. Interestingly, this result also applies to the Leslie matrix. In [section 3](#), we recall some classic results on the McKendrick equation, and prove that the eigenvectors form a complete basis. We observe numerically that the first eigenvalues of the discrete problem converge to the ones of the continuous problem.

1 Age-structured predator prey model

1.1 Predator-prey model and age-structuration

1.1.1 The predator-prey model

The predator prey model and the Lotka-Volterra equations are among the most known models in population dynamics. For the sake of exhaustiveness, let's recall the classic Lotka-Volterra equations ([Lotka, 1926](#); [Volterra, 1926](#)) :

$$\begin{cases} d_t x(t) = \alpha x(t) - \beta y(t)x(t) \\ d_t y(t) = \delta x(t)y(t) - \gamma y(t) \end{cases} \quad (1)$$

where :

- x is the number of preys,

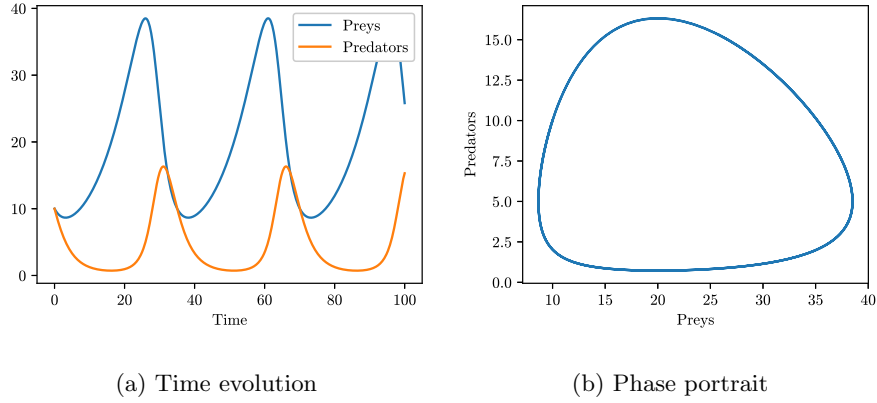


Fig. 1: Prey-predator model

- y is the number of predators,
- α is the natality rate for preys,
- β describes the effect of the presence of predators on the prey mortality rate,
- γ is the mortality rate for predators,
- δ describes the effect of the presence of preys on the predator natality rate.

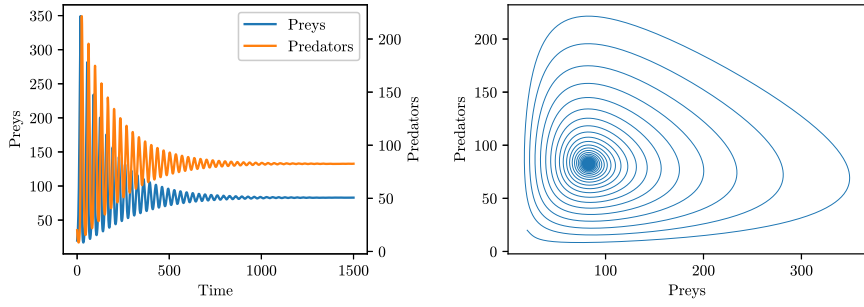
It is well known that for positive parameters $\alpha, \beta, \gamma, \delta$, the system (1) has a periodic behavior (see Figure 1).

We refer the reader to Wangersky (1978); Takeuchi (1996); Cherniha and Davydovych (2022) for detailed analyses on the Lotka-Volterra equations.

1.1.2 Age-structuration of the predator-prey model

Age-structured predator-prey models have been widely studied in the literature on population dynamics. We may cite Lu et al. (2017); Zhang and Liu (2021); Bentout et al. (2022) for recent breakthroughs on this topic.

A classic approach to reach a further level of realism consists in introducing a structuration on the age of individuals. We introduce a second, positive variable a standing for the age, a transport term as a partial age derivative and adapt the shapes of rates linked to predation. We get the system (2a)-(2f) :



(a) Time evolution

(b) Phase portrait

Fig. 2: Age-structured prey-predator model

$$\begin{cases} \partial_t x(t, a) + \partial_a x(t, a) + \left(\int_0^{+\infty} \beta(a, \tilde{a}) y(t, \tilde{a}) d\tilde{a} \right) x(t, a) = 0, & (2a) \\ \partial_t y(t, a) + \partial_a y(t, a) + \gamma(a) y(t, a) = 0, & (2b) \\ x(t, 0) = \int_0^{+\infty} \alpha(a) x(t, a) da, & (2c) \\ y(t, 0) = \int_0^{+\infty} \int_0^{+\infty} \delta(a, \tilde{a}) x(t, \tilde{a}) d\tilde{a} da, & (2d) \\ x(0, a) = x_0(a), & (2e) \\ y(0, a) = y_0(a), & (2f) \end{cases}$$

where we added initial conditions x_0 and y_0 . The reproduction terms now appear in boundary conditions (2c)-(2d), as they affect only the populations at age zero. The rates α, γ (resp. β, δ) are to be chosen with compact support in \mathbb{R}_+^* (resp. $\mathbb{R}_+^* \times \mathbb{R}_+^*$) to ensure existence and uniqueness of the solution of this system.

There exists a wide diversity of behaviors which can be observed in a such age-structured system. Contrary to (1), which had parameters in \mathbb{R}^4 , the space of parameters in (2a)-(2f) has infinite dimension. It is interesting noticing that the resulting behavior is not necessarily periodic; it may also, for example, converge to a fixed point (see Figure 2).

This figure has been computed using a semi-discretization on age and Dassault Systèmes ODE solver, Dymola. In the next subsection, we explain the step of semi-discretization.

1.2 Semi-discretization of the age-structured predator-prey model

Many approaches exist to achieve a numerical simulation of (2a)-(2f). The approach we took on consists in two steps :

1. derive from (2a)-(2f) an age semi-discretized formulation,
2. solve numerically the semi-discretized formulation thanks to ODE solvers.

We first truncate the age interval to $[0, A]$, with $A > 0$ representing a maximal age. Let consider a discretization of $[0, A]$ into N intervals $\left[a_{i-\frac{1}{2}}, a_{i+\frac{1}{2}} \right]$ for i in $0, \dots, N-1$, with $a_{-\frac{1}{2}} = 0$ and $a_{N-\frac{1}{2}} = A$. The discretization will be regular, with $\Delta a_N = a_{i+\frac{1}{2}} - a_{i-\frac{1}{2}}$ independent of i .

The choice of a numerical scheme is not the heart of our work. What follows could be adapted with any numerical scheme. For the sake of simplicity, we choose an upwind scheme, where, for i in $0, \dots, N-1$,

$$\begin{cases} x\left(t, a_{i+\frac{1}{2}}\right) \text{ is approximated by } \frac{1}{\Delta a_N} \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} x(t, a) da \\ y\left(t, a_{i+\frac{1}{2}}\right) \text{ is approximated by } \frac{1}{\Delta a_N} \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} y(t, a) da \end{cases} \quad (3)$$

We also define the aggregated population variables

$$X_i(t) = \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} x(t, a) da,$$

$$Y_i(t) = \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} y(t, a) da.$$

Applying the semi-discretization (3) to the age-structured continuous system (2a)-(2f) leads to the dynamical system (4a)-(4d).

$$\begin{cases} d_t X_i + \frac{X_i - X_{i-1}}{\Delta a_N} + \left(\sum_{k=0}^{N-1} \beta_{ik} Y_k \right) X_i = 0, & 1 \leq i \leq N-1, & (4a) \\ d_t X_0 + \frac{1}{\Delta a_N} X_0 - \sum_{k=0}^{N-1} \alpha_k X_k + \left(\sum_{k=0}^{N-1} \beta_{0k} Y_k \right) X_0 = 0, & & (4b) \\ d_t Y_i + \frac{Y_i - Y_{i-1}}{\Delta a_N} + \gamma_i Y_i = 0, & 1 \leq i \leq N-1, & (4c) \\ d_t Y_0 + \frac{1}{\Delta a_N} Y_0 - \sum_{j=0}^{N-1} \left(\sum_{k=0}^{N-1} \delta_{jk} X_k \right) Y_j + \gamma_0 Y_0 = 0, & & (4d) \end{cases}$$

where the boundary conditions (2c)-(2d) have been adapted into special terms in (4b)-(4d), as input population flows into the zero-aged class.

The discrete parameters $(\alpha_i)_{0 \leq i \leq N-1}, (\beta_i)_{0 \leq i \leq N-1}, (\gamma_i)_{0 \leq i \leq N-1}, (\delta_i)_{0 \leq i \leq N-1}$ are derived from the continuous ones :

$$\left\{ \begin{array}{l} \alpha_i = \frac{1}{\Delta a_N} \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} \alpha(a) da \\ \beta_{ij} = \frac{1}{\Delta a_N^2} \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} \int_{a_{j-\frac{1}{2}}}^{a_{j+\frac{1}{2}}} \beta(a, \tilde{a}) d\tilde{a} da \\ \gamma_i = \frac{1}{\Delta a_N} \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} \gamma(a) da \\ \delta_{ij} = \frac{1}{\Delta a_N^2} \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} \int_{a_{j-\frac{1}{2}}}^{a_{j+\frac{1}{2}}} \delta(a, \tilde{a}) d\tilde{a} da \end{array} \right.$$

The choice of functions $\alpha, \beta, \gamma, \delta$ follows usual hypotheses, which may depend on the type of ecosystem one wants to model.

1.3 Numerical observations

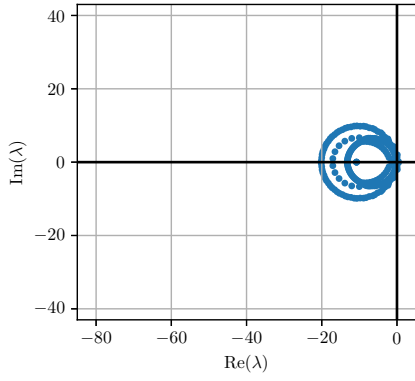
A natural step, to study the asymptotic behavior of the system (4a)-(4d), consists in studying the eigenvalues of the jacobian at an equilibrium point. To reach such an equilibrium, we may numerically run the simulation until the system seems to reach an equilibrium point, and study the jacobian at this final point. We ensure that the system has converged by numerically testing that enough points are sufficiently close before stopping the computation.

We are interested in the sign of the real part of the first eigenvalue, which characterizes the stability properties of the system. As one can easily compute, thanks to linear algebra tools, all the eigenvalues of the system (4a)-(4d), we decided to give a look at the whole spectrum, and how its shape depends on the number of age groups. We get the Figure 3.

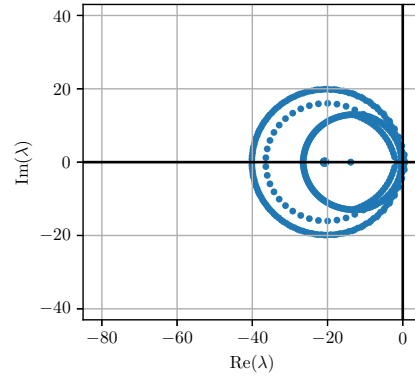
The eigenvalues distribution observed on Figure 3 is somewhat interesting, with circles tangent to the y -axis with a center which seems to translate along the x -axis, as N increases ; we also observe inner structures, which go from points to small circles as N increases.

2 Semi-discretized McKendrick equation

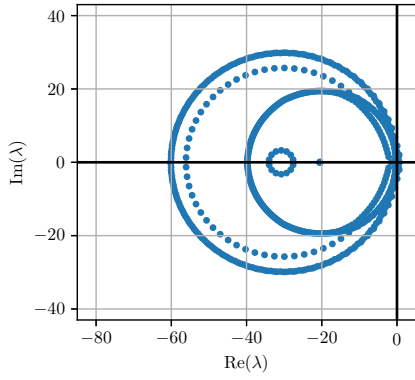
The numerical observations on Figure 3 are of interest, but the predator-prey model and the age-structured Lotka-Volterra equations are very complex to study. To simplify the problem at hand, we will study an age-structured McKendrick equation. Contrary to the predator-prey model and its nonlinearities due to predation, the McKendrick equation is linear. As a result, the infinitesimal generator in the discrete age-structured formulation is linear, so studying the stability through jacobian eigenvalues is equivalent to studying the eigenvalues of the operator itself.



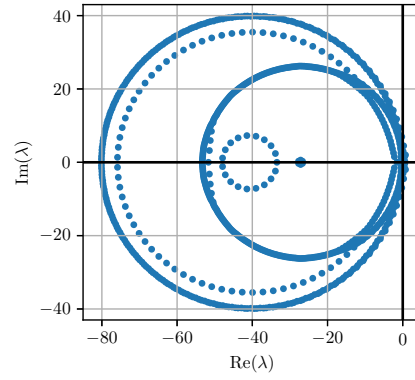
(a) $N = 100$



(b) $N = 200$



(c) $N = 300$



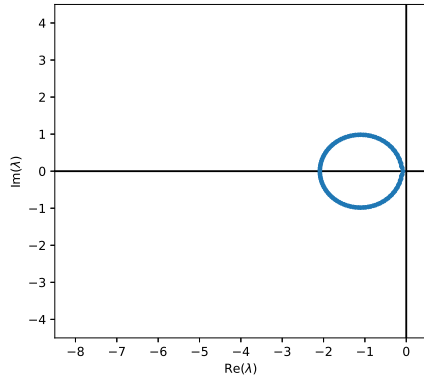
(d) $N = 400$

Fig. 3: Eigenvalues of the age-structured semi-discretized predator-prey model, at the end of the simulation, for various value of number of age groups N .

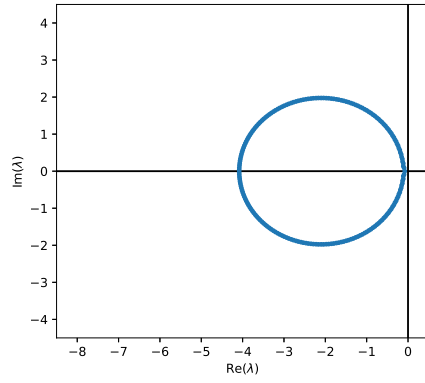
Numerically, we may formulate the following conjecture (see [Figure 4](#)) : asymptotically, the eigenvalues set in the complex plane seems to describe a circle, with center located at $\left(-\frac{1}{\Delta a_N}, 0\right)$, with radius $\frac{1}{\Delta a_N}$.

2.1 Semi-discretization

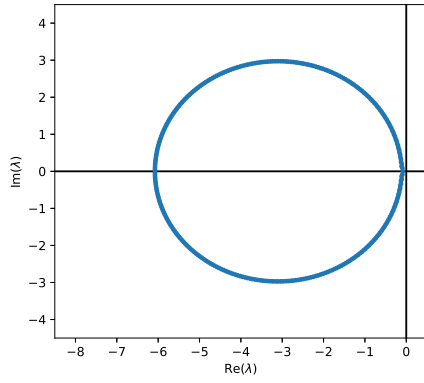
Let us recall the well-known McKendrick equation :



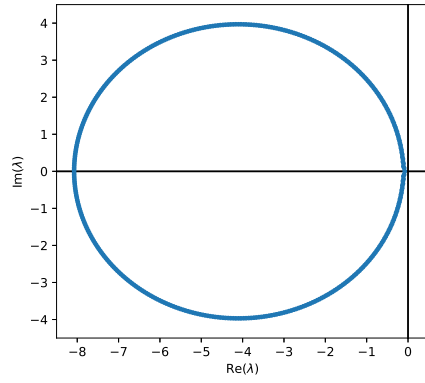
(a) $N = 100$



(b) $N = 200$



(c) $N = 300$



(d) $N = 400$

Fig. 4: Eigenvalues of the semi-discretized McKendrick equation, for various value of number of age groups N .

$$\begin{cases} \partial_t \phi(t, a) + \partial_a \phi(t, a) + \mu(a)\phi(t, a) = 0 \\ \phi(t, 0) = \int_0^{+\infty} b(a)\phi(t, a) da \\ \phi(0, a) = \phi_0(a) \end{cases} \quad (5)$$

where ϕ is the population density, μ is the death rate, b the birth rate, a the age of individuals. The semi-discretization of (5) with an upwind-scheme is straight-forward:

$$\begin{cases} d_t \psi_i + \frac{\psi_i - \psi_{i-1}}{\Delta a_N} + \mu_i \psi_i = 0 & 1 \leq i \leq N-1 \\ d_t \psi_0 + \frac{1}{\Delta a_N} \psi_0 - \sum_{k=0}^{N-1} b_k \psi_k + \mu_0 \psi_0 = 0 \end{cases} \quad (6)$$

where:

- N is the number of age groups,
- $\psi_i(t) = \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} \phi(t, a) da$, is a discrete population variable, between ages $a_{i-\frac{1}{2}}$ and $a_{i+\frac{1}{2}}$, for i in $0, \dots, N-1$, following the notations of [subsection 1.2](#),
- $b_i = \frac{1}{\Delta a_N} \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} b(a) da$,
- $\mu_i = \frac{1}{\Delta a_N} \int_{a_{i-\frac{1}{2}}}^{a_{i+\frac{1}{2}}} \mu(a) da$.

2.2 Eigenvalues problem

The eigenvalues problem associated to (6) may be written as the following:

$$\begin{cases} - \left(\frac{\psi_i - \psi_{i-1}}{\Delta a_N} + \mu_i \psi_i \right) = \lambda \psi_i & 1 \leq i \leq N-1 \end{cases} \quad (7a)$$

$$\begin{cases} - \left(\frac{1}{\Delta a_N} \psi_0 - \sum_{k=0}^{N-1} b_k \psi_k + \mu_0 \psi_0 \right) = \lambda \psi_0 \end{cases} \quad (7b)$$

where λ is a complex eigenvalues and $(\psi_i)_{0 \leq i \leq N-1}$ is an eigenvector in \mathbb{C}^N . Some steps of computation give, for i in $0, \dots, N-1$,

$$\psi_i = \frac{\psi_0}{\prod_{k=1}^i (1 + \Delta a_N (\mu_k + \lambda))}.$$

We put back this expression into (7b), which gives after simplification

$$-1 + \Delta a_N \sum_{i=0}^{N-1} \frac{b_i}{\prod_{k=0}^i (1 + \Delta a_N (\mu_k + \lambda))} = 0$$

Multiplying this equation by $\prod_{k=0}^{N-1} (1 + \Delta a_N (\mu_k + \lambda))$ gives the following characteristic equation:

$$- \prod_{k=0}^{N-1} (1 + \Delta a_N (\mu_k + \lambda)) + \Delta a_N \sum_{i=0}^{N-1} b_i \prod_{k=i+1}^{N-1} (1 + \Delta a_N (\mu_k + \lambda)) = 0 \quad (8)$$

From now, for the sake of realism, we will assume an hypothesis on fertile age groups: for any given number of age groups N set in the semi-discrete model, there exists two integers n and m such that for $i < n - m$ or $i > n$, $b_i = 0$. n is the index of the older fertile age group, m is the width of the fertile age groups range. Because the fertility age range in a population is supposed to be independent from the age structure, we will assume the existence of reals α and β , strictly between 0 and 1, such that $n \underset{N \rightarrow +\infty}{\sim} \beta N$, $m \underset{N \rightarrow +\infty}{\sim} \alpha N$. From now, we will suppose that the problem may be expressed in terms of n , and will denote Δa_N by Δa_n . We also achieve a rescaling of the eigenvalue, by setting $z = 1 + \Delta a_n \lambda$.

The characteristic equation (8) rewrites, under these assumptions,

$$\prod_{k=1}^n (z + \Delta a_n \mu_k) = \Delta a_n \sum_{i=n-m}^n b_i \prod_{k=i+1}^n (z + \Delta a_n \mu_k) \quad (E_n)$$

2.3 Asymptotic distribution of eigenvalues

We now present our main result on the circular distribution of eigenvalues for the semi-discretized McKendrick equation.

To achieve that, we assume an additional and strong hypothesis: the birth and death rates are piecewise-constant. This assumption is, to be sure, restrictive, but adapted to the shape of data on birth rates and death rates we get from official statistical institutes. In a perspective of numerical simulation and model calibration, this hypothesis is not much restrictive.

Theorem 1 (Asymptotic properties of eigenvalues of (E_n)). *We assume piecewise-constant birth and death rates. Then we get the following results:*

1. Let $(z_n)_{n \in \mathbb{N}}$ be a sequence of solutions of (E_n) . Then

$$\lim_{n \rightarrow +\infty} |z_n| = 1$$

2. For any $z_0 = e^{i\theta_0}$ in \mathbb{U} , there exists a sequence $(z_n)_{n \in \mathbb{N}}$ of solutions to (E_n) converging to z_0 .

This theorem shows a result of density of the solutions to (E_n) in the unit circle. We provide below a sketch of demonstration.

- Proof.* 1. • Let $R = \limsup_{n \rightarrow +\infty} |z_n|$. We prove by contradiction that $R \leq 1$. If $R > 1$, we may show the existence of a sequence $(u_n)_{n \in \mathbb{N}}$, converging to 1, such that for n large enough,

$$\left(\frac{R+1}{2} \right)^{1-\alpha} \leq |z_n| \leq u_n$$

This is a contradiction, as $\left(\frac{R+1}{2}\right)^{1-\alpha} > R > 1$.

- We prove by contradiction that $R \geq 1$. If not, we can extract a subsequence, still denoted by $(z_n)_{n \in \mathbb{N}}$, such that $|z_n|$, which converges to a $L < 1$. Under the piecewise-constant hypothesis, the following computation holds on (E_n) :

$$\prod_{k=1}^n (z_n + \Delta a_n \mu_k) = \Delta a_n \sum_{j=0}^{K-1} C_j \sum_{i=jp_n}^{(j+1)p_n-1} \left(\prod_{l=0}^{j-1} (z_n + \Delta a_n M_l)^{p_n} \right) (z_n + \Delta a_n M_j)^{i-jp_n},$$

where K is the number of subintervals on which b and μ are constant, p_n the number of age groups on each subinterval, and C_j (resp. M_j) is the common value of b_{n-i} (resp. μ_{n-i}) for i between jp_n and $(j+1)p_n - 1$,

$$\prod_{j=0}^{K-1} \prod_{k=jp_n}^{(j+1)p_n-1} (z_n + \Delta a_n \mu_{n-k}) = \Delta a_n \sum_{j=0}^{K-1} C_j \left(\prod_{l=0}^{j-1} (z_n + \Delta a_n M_l)^{p_n} \right) \frac{(z_n + \Delta a_n M_j)^{p_n} - 1}{z_n + \Delta a_n M_j - 1},$$

$$\prod_{j=0}^{K-1} (z_n + \Delta a_n M_j)^{p_n} = \Delta a_n \sum_{j=0}^{K-1} C_j \left(\prod_{l=0}^{j-1} (z_n + \Delta a_n M_l)^{p_n} \right) \frac{(z_n + \Delta a_n M_j)^{p_n} - 1}{z_n + \Delta a_n M_j - 1}.$$

We know that

$$\Delta a_n \sim \frac{A\beta}{n}$$

and that for $j \neq 0$, $\prod_{l=0}^{j-1} (z_n + \Delta a_n M_l)^{p_n}$ converges to 0 as well as $(z_n + \Delta a_n M_j)^{p_n}$. Then we may extract a subsequence, still denoted by $(z_n)_{n \in \mathbb{N}}$, and have a real C such that

$$\prod_{j=0}^{K-1} (z_n + \Delta a_n M_j)^{p_n} = \frac{C}{n} + o\left(\frac{1}{n}\right)$$

Taking the logarithm of each member gives

$$\sum_{j=0}^{K-1} \ln |z_n + \Delta a_n M_j| = \frac{\ln(C) - \ln(n)}{p_n} + o(1).$$

As

$$\sum_{j=0}^{K-1} \ln |z_n + \Delta a_n M_j| \leq K \ln(C) < 0$$

and

$$\lim_{n \rightarrow +\infty} \frac{\ln(C) - \ln(n)}{p_n} \xrightarrow{n \rightarrow +\infty} 0,$$

we get a contradiction.

2. We denote the average mortality rate $\frac{1}{n} \sum_{k=1}^n \mu_k$ by $\bar{\mu}$ and rewrite (E_n) as a fixed point equation:

$$\left(z + \frac{\bar{\mu}}{n}\right)^n = \left(z + \frac{\bar{\mu}}{n}\right)^n - \prod_{k=1}^n \left(z + \frac{\mu_k}{n}\right) + \frac{C}{n} \sum_{i=0}^m b_{n-i} \prod_{k=n-i+1}^n \left(z + \frac{\mu_k}{n}\right), \quad (9)$$

where $C = A\beta$.

We prove the existence of a solution to (9) (and consequently, to (E_n)) in the angular sector \mathcal{D}_{n,θ_0} defined by

$$\mathcal{D}_{n,\theta_0} = \left\{ z \in \mathbb{C}, |z| \in [0, 2], \arg(z) \in \left[\theta_0 - \frac{\pi}{n}, \theta_0 + \frac{\pi}{n} \right] \right\}.$$

In order to apply the Brouwer fixed point theorem², we draw a bijection ξ_n between \mathcal{D}_{n,θ_0} and $\overline{\mathcal{D}}(0, 2)$,

We rewrite (9) as

$$\left(z + \frac{\bar{\mu}}{n}\right)^n = \varphi_n(z) \quad (10)$$

and denote by χ_n a monovaluation of the inverse of the map $z \mapsto z^n$. We then rewrite (10) as

$$\tilde{z} = \xi_n \left(\chi_n \circ \varphi_n \circ \xi_n^{-1}(\tilde{z}) - \frac{\bar{\mu}}{n} \right) \quad (11)$$

where $\tilde{z} = \xi_n(z)$ belongs to $\overline{\mathcal{D}}(0, 2)$. The right-hand side of (11) is denoted by $f_n(\tilde{z})$ so that a stronger form of (9) is equivalent to

$$f_n(\tilde{z}) = \tilde{z}, \quad (12)$$

One can easily show that f_n is continuous. It remains to prove that $\overline{\mathcal{D}}(0, 2)$ is stable by f_n . We have, on the last term of $\varphi_n(z)$, for z in $\overline{\mathcal{D}}(0, 2)$, the following estimation:

$$\left| \frac{C}{n} \sum_{i=0}^m b_{m-i} \prod_{k=n-i+1}^n \left(z + \frac{\mu_k}{n}\right) \right| = \left(2 + \frac{\|\mu\|_\infty}{n} \right)^{m+1} \mathcal{O}\left(\frac{1}{n}\right)$$

²see e.g. Boothby (1971) for details and demonstration

The two first terms of $\varphi_n(z)$ are rewritten as

$$\left(z + \frac{\bar{\mu}}{n}\right)^n - \prod_{k=1}^n \left(z + \frac{\mu_k}{n}\right) = \left(z + \frac{\bar{\mu}}{n}\right)^n \left(1 - \frac{\prod_{k=1}^n \left(z + \frac{\mu_k}{n}\right)}{\left(z + \frac{\bar{\mu}}{n}\right)^n}\right),$$

and after some computation, the following estimation holds:

$$\frac{\prod_{k=1}^n \left(z + \frac{\mu_k}{n}\right)}{\left(z + \frac{\bar{\mu}}{n}\right)^n} = 1 + O\left(\frac{1}{n}\right),$$

so that

$$|\varphi_n(z)| \leq O\left(\frac{1}{n}\right) \left(\left(2 + \frac{\bar{\mu}}{n}\right)^n + \left(2 + \frac{\|\mu\|_\infty}{n}\right)^{m+1} \right).$$

One can then prove the existence of a $C_1 > 0$ such that, for n large enough,

$$|\varphi_n(z)| \leq \frac{2C_1}{n} \left(2 + \frac{\|\mu\|_\infty}{n}\right)^n,$$

$$|\chi_n \circ \varphi_n(z)| \leq (2C_1)^{\frac{1}{n}} \left(2 + \frac{\|\mu\|_\infty - 2\ln(n)}{n} + o\left(\frac{\ln(n)}{n}\right)\right),$$

$$\left| \xi_n \left(\chi_n \circ \varphi_n(z) - \frac{\bar{\mu}}{n} \right) \right| \leq 2 + \frac{\|\mu\|_\infty 2\ln(2C_1) + \bar{\mu} - 2\ln(n)}{n} + o\left(\frac{\ln(n)}{n}\right),$$

and then conclude that $f_n(z) \in \overline{\mathcal{D}}(0, 2)$.

By applying Brouwer's fixed point theorem, we then get a solution of (12), which provides by applying ξ_n backwards a solution of (9) which belongs to $\mathcal{D}_{n, \theta_0}$, *i.e.* which has argument converging to θ_0 as n goes to infinity.

The conjugation of the two steps shows that the constructed sequence $(z_n)_{n \in \mathbb{N}}$ converges to z_0 as n goes to infinity. □

We can verify that the piecewise regularity assumption of [Theorem 1](#) is also crucial here. We can construct counter-examples that give us eigenvalues inside the unit disk, even with a large number of age groups, by taking random uniform identically distributed values of natality or mortality between 0 and 1 (see [Figure 5](#)).

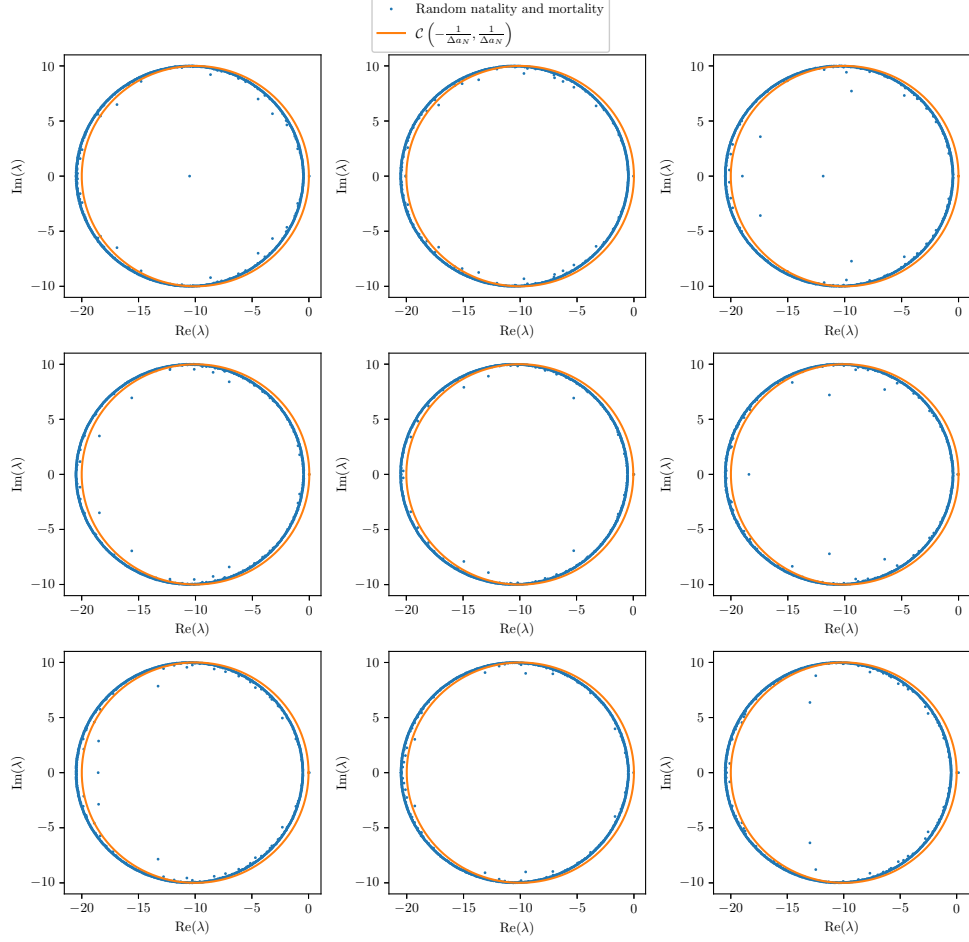


Fig. 5: Computation of eigenvalues of (7a)-(7b) with random natality and mortality values, with $N = 1000$ age groups. The target circle is represented for reference.

2.4 Relation with the Leslie matrix

In this subsection, we are interested in the dynamic of a population P divided into N age groups. The dynamic is ruled by the following recurrence equation:

$$P(t + \Delta t) = LP(t) \quad (13)$$

where Δt represents a time step and $P(t)$ is a vector of \mathbb{R}^N with, for age group i , $P(t)_i$ the population of the i^{th} age group. In the litterature, the matrix L is called the

Leslie matrix (Leslie, 1945). It is a non-negative matrix given by

$$L = \begin{pmatrix} \Delta t b_0 & \cdots \cdots & \cdots & \Delta t b_{N-1} \\ 1 - \Delta t \mu_0 & 0 & \cdots & 0 \\ 0 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & 1 - \Delta t \mu_{N-2} & 0 \end{pmatrix}$$

We first recall a classic result on the spectrum of the Leslie Matrix, which is an application of the Perron-Frobenius theorem.

Theorem 2. *The Leslie Matrix has one real eigenvalue which is equal to its spectral radius.*

Obviously there is a strong link between the Leslie matrix and the matrix of the dynamic system (6) resulting from the semi-discretization of the McKendrick equation, which will be denoted by M . Taking $\Delta a_N = \Delta t$ gives

$$M = \begin{pmatrix} \frac{1}{\Delta t} + \mu_0 - b_0 & -b_1 & \cdots & \cdots & -b_{N-1} \\ -\frac{1}{\Delta t} & \frac{1}{\Delta t} + \mu_1 & 0 & \cdots & 0 \\ 0 & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & -\frac{1}{\Delta t} & \frac{1}{\Delta t} + \mu_{N-1} \end{pmatrix}$$

We denote by J the following matrix:

$$J = \begin{pmatrix} \mu_0 & 0 & \cdots & \cdots & 0 \\ -\mu_0 & \mu_1 & 0 & \cdots & 0 \\ 0 & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & 0 \\ 0 & \cdots & 0 & -\mu_{N-2} & \mu_{N-1} \end{pmatrix}$$

Then one immediately sees that

$$\frac{P(t + \Delta t) - P(t)}{\Delta t} = \frac{L - I_N}{\Delta t} P(t) = (-M + J)P(t)$$

so that

$$L = I_N - \Delta t M + \Delta t J$$

As $\Delta t J = O(\Delta t)$, the Leslie Matrix L is a perturbation of matrix $I_N - \Delta t M$, and we have, as Δt goes to 0, L close to $I_N - \Delta t M$.

It follows from Theorem 1 that $I_N - \Delta t M$ is a matrix whose eigenvalues are close to the unit circle when N is high enough. Consequently, the eigenvalues of L will also be close to the unit circle (as the map $\lambda \mapsto 1 - \Delta t \lambda$ is precisely the rescaling operation applied to the eigenvalues of M).

3 McKendrick equation spectrum

Let us recall the McKendrick equation introduced in the previous section:

$$\begin{cases} \partial_t \phi(t, a) + \partial_a \phi(t, a) + \mu(a)\phi(t, a) = 0 \\ \phi(t, 0) = \int_0^{+\infty} b(a)\phi(t, a) da \\ \phi(0, a) = \phi_0(a) \end{cases} \quad (5)$$

and the assumptions presented in the introduction: b is zero out of a fertility interval $[a_0, a_1]$, and for any $t \geq 0$, $\phi(t, \cdot)$ is zero out of an age interval $[0, A]$, where $A > 0$ is the maximum age. The boundary term may then be rewritten $\int_{a_0}^{a_1} b(a)\phi(t, a) da$. For what follows, we will also assume that the mortality coefficient $\mu(t, a)$ and the natality coefficient $b(t, a)$ are non-negative $L^\infty(]0, A[)$ functions.

It is well known that the problem (5) is well posed. Moreover, one can exhibit an analytical solution.

Theorem 3 (Analytical solution of McKendrick equation). *There exists one unique solution to the McKendrick equation. Moreover, if the infertility interval is such that $0 < a_0 < a_1 < A < +\infty$, then the solution is given by the following analytical formula, for all $t < a_0$:*

$$\phi(t, a) = \mathbf{1}_{a > t} \psi_I(t, a) + \mathbf{1}_{a \leq t} \psi_B(t, a)$$

with

$$\psi_I(t, a) = \phi_0(a - t) \exp\left(\int_0^t -\mu(u, a - t + u) du\right)$$

and

$$\psi_B(t, a) = \left(\int_{a_0}^{a_1} \psi_I(t - a, \tilde{a}) da\right) \exp\left(-\int_{t-a}^t \mu(u, a - t + u) du\right)$$

By recurrence, the formula can be extended on each time intervals of the form $[ia_0, (i+1)a_0[$.

In what follows, the parameters μ and b will be independent of the time. Let us introduce the following spectral problem in $L^2(]0, A[)$ associated with problem (5), where the infinite bound in the natality term may be replaced by A :

$$\begin{cases} -d_a \phi(a) - \mu(a)\phi(a) = \lambda \phi(a), \\ \phi(0) = \int_0^A b(a)\phi(a) da. \end{cases} \quad (14)$$

This problem is not self-adjoint, and as often in this kind of situation, it is useful to introduce its adjoint spectral problem

$$\begin{cases} d_a \phi^*(a) - \mu(a)\phi^*(a) + b(a)\phi^*(0) = \lambda^* \phi^*(a), \\ \phi^*(A) = 0. \end{cases} \quad (15)$$

The eigenvectors of the problems (14) and (15), if they exist, can be computed explicitly. Indeed, if (λ, ϕ) is an eigenpair solution of (14), then

$$\phi(a) = \phi(0) \exp \left(- \int_0^a (\lambda + \mu(\tilde{a})) \, d\tilde{a} \right).$$

Moreover, the eigenvalue λ is solution of the following characteristic equation, which is obtained from the boundary condition:

$$1 = \int_0^A b(a) \exp \left(- \int_0^a (\lambda + \mu(\tilde{a})) \, d\tilde{a} \right) \, da. \quad (16)$$

If (λ^*, ϕ^*) is an eigenpair solution of (15), then

$$\phi^*(a) = \phi^*(0) \int_a^A b(\tilde{a}) \exp \left(- \int_a^{\tilde{a}} (\lambda^* + \mu(\tilde{\tilde{a}})) \, d\tilde{\tilde{a}} \right) \, d\tilde{a}$$

and the eigenvalue satisfies the same characteristic equation (16) as the direct problem. We shall see later more complete results on the eigenpairs of problems (14) and (15). Let us say for now that there exists a unique real eigenvalue to (14), often called the first or leading eigenvalue, which is associated with a positive eigenvector. The reason why the spectral problem is important is that the global dynamic of the population will be dictated by the sign of the real part of the first eigenvalue of problem (14).

Theorem 4. *Let (λ_1, ϕ_1) denote the first eigenpair of problem (14). Then for any $\varepsilon > 0$, there exists a constant c and a time T such that for any $t > T$, we have*

$$\|\phi(t, \cdot) - \langle \phi_1^*, \phi_I \rangle \exp(\lambda_1 t) \phi_1\|_{L^2([0, A])} \leq c \exp((\lambda_1 - \varepsilon)t).$$

For a proof of this proposition, the reader will usefully read [Song, J. et al. \(1982\)](#).

3.1 Compactness of the McKendrick operator

We study the compact nature of the McKendrick operator T , defined in the [Equation 5](#) below.

Theorem 5. *The operator T , defined by*

$$T : \begin{pmatrix} L^2([0, A]) & \rightarrow & L^2([0, A]) \\ f & \mapsto & \phi \end{pmatrix},$$

where ϕ is solution of

$$\begin{cases} d_a \phi(a) + \mu(a) \phi(a) = f(a), \\ \phi(0) = \int_0^A b(a) \phi(a) \, da, \end{cases} \quad (17)$$

is compact. Its eigenvalues are the inverse of the eigenvalues of (14). Moreover, T is positive.

Proof. The analytical solution of problem (17) is given by the following formula:

$$\phi(a) = \left(\phi(0) + \int_0^a \exp \left(\int_0^s \mu(v) dv \right) f(s) ds \right) \exp \left(- \int_0^a \mu(s) ds \right),$$

with

$$\phi(0) \left(1 - \int_0^A b(a) \exp \left(- \int_0^a \mu(s) ds \right) da \right) = \int_0^A b(a) \int_0^a \exp \left(\int_a^s \mu(v) dv \right) f(s) ds da.$$

From this the following *a priori* estimates can be clearly obtained:

$$\begin{cases} |\phi(0)| \leq C \|f\|_2, \\ \|\phi\|_2 \leq C \|f\|_2, \\ \|d_a \phi\|_2 \leq C \|f\|_2. \end{cases}$$

This ensures the compactness of T . In fact, it is possible that the factor $1 - \int_0^A b(a) \exp \left(- \int_0^a \mu(s) ds \right) da$ is equal to 0. In this situation, the right-hand side term must also be equal to 0. Notice that 0 is then the real eigenvalue of problem (14), and that the condition satisfied by f precisely corresponds to the Fredholm alternative. The solution of (17) will be defined up to a function proportional to the eigenvector associated with the null eigenvalue. In the L^2 space quotiented by the first eigenspace, the *a priori* estimate will still hold. Then the derivative will also be bounded, and the compactness ensured. The positivity is obvious considering the analytical formula. \square

The compactness of operator T allows using the following classic functional analysis theorem which gives us information on the eigenvalues and eigenvectors of problem (14) (see for instance Kato (1995)).

Theorem 6. *Let T be a compact operator. Then its spectrum is at most a countable set, with no accumulation point different from 0. Each nonzero value λ of the spectrum is an eigenvalue of T of finite multiplicity. The conjugate value $\bar{\lambda}$ is an eigenvalue of the adjoint operator T^* with the same multiplicity.*

3.2 Spectral properties

Finally, let us write a summary of the results that are known on the problems (14) and (15). A demonstration of these results can again be read in Song, J. et al. (1982).

Theorem 7 (Spectral properties McKendrick equation). • *The spectral problems (14) and (15) have one and only one real eigenvalue, solution of the characteristic equation (16).*

- *All the other eigenvalues arise as pairs of complex and conjugate numbers. Their real part is greater than the real part of the unique real eigenvalue.*
- *There exists at most a countable number of eigenpairs.*
- *If there is an infinity of eigenvalues, their module tends to infinity.*

- If we denote by (λ_k, ϕ_k) and $(\overline{\lambda}_k, \phi_k^*)$ the eigenpairs of (14) and (15), then these eigenvectors can be normalized so that they are orthogonal:

$$\langle \phi_l^*, \phi_k \rangle = \delta_{kl}$$

- In every vertical strip of finite width, there exists at most a finite number of eigenvalues.

Of course, one question remains unanswered. Do the eigenvectors of problem (14) form a complete basis? As in the heat equation for instance, we would like to know if we can write for any $f \in L^2(]0, A[)$:

$$\left\{ \begin{array}{l} f = \sum_{k=0}^{+\infty} \langle \phi_k^*, f \rangle \phi_k, \\ Tf = \sum_{k=0}^{+\infty} \frac{1}{\lambda_k} \langle \phi_k^*, f \rangle \phi_k. \end{array} \right.$$

We will show that this result is true.

Theorem 8. *The eigenvectors of the spectral problem (14) form a complete basis of the space $L^2(]0, A[)$.*

Proof. The operator T is a compact operator. Consequently, its spectrum is at most countable and the following decomposition holds for any meromorphic function f (see [Riechers and Crutchfield \(2018\)](#) for instance):

$$f(T) = \sum_{\lambda \in \Lambda_T} \frac{1}{2i\pi} \oint_{C_\lambda} f(z) (zI - T)^{-1} dz,$$

where the sum runs over the values in the spectrum Λ_T of T , and C_λ is a contour encircling the isolated eigenvalue λ . For $f = I$, this yields

$$T = \sum_{\lambda \in \Lambda_T} \lambda \frac{1}{2i\pi} \oint_{C_\lambda} (zI - T)^{-1} dz + \frac{1}{2i\pi} \oint_{C_\lambda} (z - \lambda) (zI - T)^{-1} dz \quad (18)$$

Let us introduce the following operators

$$T_{\lambda,0} = \frac{1}{2i\pi} \oint_{C_\lambda} (zI - T)^{-1} dz,$$

$$T_{\lambda,1} = \frac{1}{2i\pi} \oint_{C_\lambda} (z - \lambda) (zI - T)^{-1} dz.$$

The operator $T_{\lambda,0}$ is a projection operator on the eigenspace corresponding to the eigenvalue λ , and $T_{\lambda,1}$ a nilpotent operator. The decomposition formula (18) is the so-called Dunford decomposition. We know explicitly the formula for the eigenvectors corresponding to a given eigenvalue. Obviously, any eigenspace is of dimension 1.

Consequently, if the nilpotent term is in fact null, the Dunford decomposition implies that there is an infinite number of eigenvalues, and that their eigenspaces form a complete basis allowing to decompose the identity and to diagonalize the operator T . It remains to see if the nilpotent term is indeed null. Remembering that the eigenvalues of T are the inverse of the eigenvalues introduced in (14), we want to know if we can find a solution f to the equation

$$\left(T - \frac{1}{\lambda_k} I\right) f = \phi_k,$$

where $T\phi_k = \frac{1}{\lambda_k}\phi_k$. Then the Fredholm alternative implies that $\langle \phi_k^*, \phi_k \rangle = 0$ which is not true since its value is equal to 1. Thus, the nilpotent space is null, which concludes the proof. \square

To end this section, let us give two numerical examples. In the first example, the natality and mortality rates are constant. It is easy then to compute the eigenvectors once the eigenvalues are known. The eigenvalues however must be calculated numerically. We will denote this set of eigenvalues by “continuous spectrum”. The spectrum displays a very classic cusp shape as can be seen on Figure 6.

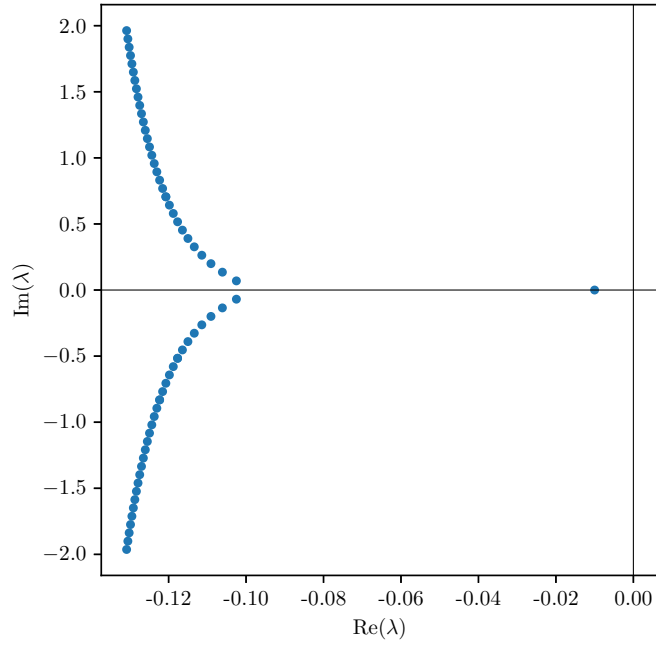


Fig. 6: Complex eigenvalues of the problem (14), with constant natality and mortality rates.

Plotting on the same figure both discrete and continuous spectrums shows an interesting link between the two problems. At a large scale, it seems that the continuous spectrum is tangent to the circle constituting the discrete spectrum (Figure 7a). At a small scale, we observe a correspondence in the shapes of the two spectrums. Indeed, the convergence of the discrete spectrum to a circle seems to be nonuniform, as the discrete spectrum presents the characteristic cusp shape (Figure 7b). This observation paves the way to a deeper study of the links between discrete and continuous spectrums. The conjecture that the continuous spectrum can be obtained from the discrete one, taking the limit on the number of age groups, seems to be reasonable.

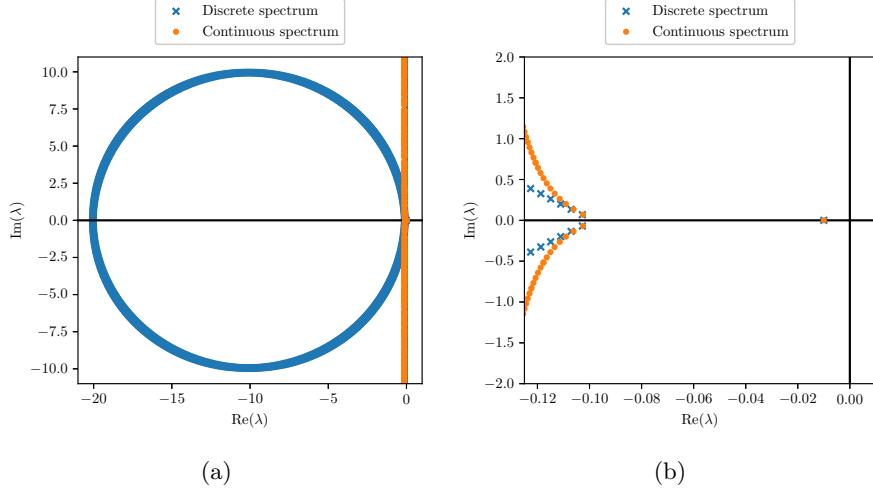


Fig. 7: Continuous and discrete spectrums of the McKendrick equation

In the second example, the mortality is constant, but the natality is concentrated in a Dirac operator $b(a) = b\delta_{a=a_0}$. Then the eigenpairs are given by

$$\begin{cases} \lambda_k = \mu - \frac{\log(b)}{a_0} + i\frac{2k\pi}{a_0} \\ \phi_k(a) = \exp\left(\left(\mu - \frac{\log(b)}{a_0} + i\frac{2k\pi}{a_0}\right)a\right) \end{cases}$$

so that we could say that the eigenvectors form a Fourier basis. The evolution problem has periodic solutions, up to a multiplicative growing or decaying exponential term. Interestingly, this situation is not at all a pure mathematical curiosity, as such reproduction strategies are employed by certain species, like some bamboo species that have a cycle of decades.

Discussion

In this paper, we present theoretical and numerical studies on a semi-discretized McKendrick equation eigenvalues. This work aims at enlightening a specific phenomenon

occurring with the distribution of the eigenvalues of the McKendrick semi-discretized equation. Although we managed to demonstrate the numerical conjectures, the theoretical results do not exhaust the issue. One could seek a deeper explanation on why such figures arise when the number of age groups goes to infinity. Moreover, what influence does the numerical scheme or the equation itself have on the discrete spectrum? How could one link the spectra of discrete and continuous McKendrick equation? What extension could one draw with the predator-prey model, or even other population models?

Future work

As presented in the previous discussion, many interesting topics arise from our study. The generalization of such theoretical results to an age-structured Lotka-Volterra model, and in a larger way, to this type of equations (*i.e.* transport equations with exchange terms) is one of these topics. To achieve that, one could linearize the age-structured Lotka-Volterra model at an equilibrium point, to get the spectrum of the continuous problem and compare it with the discrete one. Other numerical schemes could produce similar theoretical and numerical results. Understanding better the computation and characterization of equilibrium points, and handling the nonlinearities of the predator-prey model which were eclipsed in the McKendrick equation, represents a crucial issue. It would also be a topic of interest to deepen the interpretation and analysis of the eigenvalues distribution; especially, explain why circles appear with the discrete formulation and not with the continuous one, and how one can properly get the second spectrum from the first by taking the limit on the number of age groups.

Conclusion

In this work, we presented numerical and theoretical considerations on spectral properties of population dynamics models. We took simple and academic population dynamics models with an age structure, starting from predator-prey models extended within a McKendrick formalism, then undergoing a semi-discretization process. We proved a density result on the discrete formulation's eigenvalues, as the number of age groups goes to infinity. We showed the property that the eigenfunctions of McKendrick spectral problem form a complete basis of the space $L^2(]0, A[)$.

These considerations enlighten the stability analysis of such population models, where the eigenvalues distribution play a fundamental role.

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- The authors certify that they do not have any conflict of interest.
- The authors have no financial or non-financial interests to disclose.

- The authors provide their full consent for publication.

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