Novel Stochastic McKendrick-von Foerster Models with Applications

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The deterministic McKendrick-von Foerster model

$$\frac{\partial u}{\partial t}+\frac{\partial u}{\partial a}=-m(t,a)u \ \ (t,a\geq 0) \tag{1}$$

is widely used to examine age-structured populations [2,4,6]. It is usually equipped with the initial condition

$$u(0,a)=\chi(a)\geq 0$$

and the non-local boundary condition

$$u(t,0)=b(t)=\int\limits_0^\infty \beta(t,a)u(t,a)\,da\geq 0.$$

Here $u(t,a)$ is the size (density) of a certain population of a given age $a\geq 0$ at time $t\geq 0$, $m(t,a)\geq 0$ is the per capita mortality rate and $b(t)$ is the birth function that depends on the age-structured size of the population and the per capita birth rate $\beta(t,a)$.

Eq. (1) is a balance equation that can be derived from the basic biophysical principles by letting the increments in time and age be infinitely small and under the assumption that the population is isolated. This explains why the McKendrik-von Foester equation is a source of many specific population models. However, this equation does not take into account stochastic effects, like demographic and environmental fluctuations, which are of importance in any realistic description of population dynamics.

In this presentation, the following stochastic version of this model

$$\frac{\partial u}{\partial t}+\frac{\partial u}{\partial a}=-(m(t,a)+\dot{\nu}(t))u \ \ (t,a\geq 0) \tag{2}$$

is considered. Here $\dot{\nu}(t)$ is a stochastic noise which is represented by the formal (generalized) derivative of a continuous scalar stochastic process $\nu(t)$ defined on the given filtered probability space

$$\big(\Omega,\mathcal{F},(\mathcal{F}_t)_{t\geq 0},\mathbf{P}\big)$$

with the probability measure $\mathbf{P}$ on the σ-algebra $\mathcal{F}$ of subsets of Ω and an increasing sequence of σ-subalgebras $\mathcal{F}_t$ of $\mathcal{F}$, where all the introduced σ-algebras are complete with respect to the measure $\mathbf{P}$.

The aim of the presentation is to deduce the equations for the total size of the juveniles $J(t)$ and the adults $A(t)$

$$J(t)=\int_0^{\tau} u(t,a)\,da \ \text{ and } \ A(t)=\int_{\tau}^{\infty} u(t,a)\,da, \tag{3}$$

where $\tau\geq 0$ is the maturation time [6].

In the assumptions below, the following definition is used.

Definition. A real-valued (deterministic) function $\alpha(t,x,y)$, $t\geq 0$, $x,y\in(-\infty,\infty)$ belongs class L if it is measurable (as a function of three variables) and satisfies the uniform Lipschitz condition with respect to x and y:

$$\big|\alpha(t,x_1,y_1)-\alpha(t,x_2,y_2)\big|\leq L\big(|x_1-y_1|+|x_2-y_2|\big)$$

for all $t\geq 0$, $x,y\in(-\infty,\infty)$.

The restrictions on the coefficients in (2) can be summarized as follows:

(A1) The mortality rate $m(t,a)$ is defined as

$$m(t,a)=\begin{cases} m_J(t):=\mu_J(t,J(t),A(t)), & 0\leq a<\tau,\\ m_A(t):=\mu_A(t,J(t),A(t)), & a\geq\tau,\end{cases} \tag{4}$$

where μ_J and μ_A are class L functions (that is, they are independent of the age a) and $\tau\geq 0$ is the maturation time.

(A2) The function $\chi(a)\geq 0$ (the initial age distribution at time $t=0$) is càdlàg and satisfies the condition

$$\int_0^{\infty}\sup_{s\geq a}\chi(s)\,da<\infty.$$

In practical applications, the function χ has a compact support, so that this assumption will be trivially satisfied.

(A3) At any time t, the birth rate function β is defined as

$$\beta(t,a)=\begin{cases} 0, & 0\leq a<\tau,\\ \beta_A(t):=\beta_A(t,J(t),A(t)), & a\geq\tau,\end{cases}$$

where β_A is a class L function independent of the age a, and by definition, the birth rate of the juvenile population (i.e. β_J) is equal to 0.

(A4) The stochastic process ν is defined as

$$\nu(t)=\int_0^t \gamma(s,J(s),A(s))\,dB(s),$$

where B is the scalar Brownian motion and γ is a class L function.

Below is the main result of the presentation.

Theorem 1. *If assumptions* (A1)–(A4) *are fulfilled, then the aggregated age variables* (3)*, together with the auxiliary variable $X(t)$, satisfy the system*

$$
\begin{aligned}
dJ(t) = {} & \beta_A(t,J(t),A(t))A(t)\,dt - \mu_J(t,J(t),A(t))J(t)\,dt \\
& - \mathcal{D}\big\{t,J(\,\cdot\,),A(\,\cdot\,),X(\,\cdot\,)\big\}\beta_A\big(t-\tau,J(t-\tau),A(t-\tau)\big)A(t-\tau)\,dt \\
& + \gamma(t,A(t),J(t))J(t)dB(t) \ \ (t\geq\tau), \\
dA(t) = {} & -\mu_A(t,J(t),A(t))A(t)\,dt \\
& + \mathcal{D}\big\{t,J(\,\cdot\,),A(\,\cdot\,),X(t)\big\}\beta_A\big(t,J(t-\tau),A(t-\tau)\big)A(t-\tau)\,dt \\
& + \gamma(t,J(t),A(t))A(t)dB(t) \ \ (t\geq\tau), \\
dX(t) = {} & \gamma(t,J(t),A(t))X(t)\,dB(t),
\end{aligned}
\tag{5}
$$

where

$$
\mathcal{D}\big\{t,J(\,\cdot\,),A(\,\cdot\,),X(\,\cdot\,)\big\} = \exp\bigg\{-\int\limits_{t-\tau}^{t}\mu_J(s,J(s),A(s))\,ds\bigg\}X(t)X^{-1}(t-\tau)
$$

is an integral operator standing for the distributed delay in the equation.

This system satisfies the initial conditions

$$
J(t)=J_0(t), \ \ A(t)=A_0(t), \ \ X(t)=X_0(t) \ \ (t\in[0,\tau]),
$$

where $J_0(\,\cdot\,)$, $A_0(\,\cdot\,)$ and $X_0(t)$ are $\mathcal{F}_\tau$-measurable, continuous stochastic processes satisfying the following system of stochastic integro-differential equations on the interval $[0,\tau]$*:*

$$
\begin{aligned}
dJ_0(t) = {} & -\mathcal{D}\big\{t,J_0(\,\cdot\,),A_0(\,\cdot\,)\big\}\,dt + \beta_A(t,J_0(t),A_0(t))A_0(t)\,dt - \mu_J(t,J_0(t),A_0(t))J_0(t)\,dt \\
& + \gamma(t,A_0(t),J_0(t))J_0(t)\,dB(t), \\
dA_0(t) = {} & \mathcal{D}\big\{t,J_0(\,\cdot\,),A_0(\,\cdot\,)\big\}\,dt - \mu_A(t,J_0(t),A_0(t))A_0(t)\,dt \\
& + \gamma(t,J_0(t),A_0(t))A_0(t)\,dB(t), \\
dX_0(t) = {} & \gamma(t,J_0(t),A_0(t))X_0(t)\,dB(t),
\end{aligned}
$$

and

$$
\mathcal{D}_0\big\{t,J_0(\,\cdot\,),A_0(\,\cdot\,),X_0(\,\cdot\,)\big\} = \chi(\tau-t)\exp\bigg\{-\int\limits_0^t\mu_J(s,J_0(s),A_0(s))\,ds\bigg\}X_0(t).
$$

The initial conditions for the latter system are given by

$$
\begin{gathered}
J(0) = \int\limits_0^\tau u(0,s)\,ds = \int\limits_0^\tau \chi(s)\,ds, \\
A(0) = \int\limits_\tau^\infty u(0,s)\,ds = \int\limits_\tau^\infty \chi(s)\,ds, \\
X(0) = 1.
\end{gathered}
$$

The proof of this result can be found in [5].

Consider some biologically important stochastic models which can be obtained from Theorem 1.

Example 1: the stochastic counterpart of the recruitment-delayed model.
The following equation is widely used in population dynamics (see, e.g., the monograph [3] or the review paper [1]):
$$A'(t)=\mathcal{B}(A(t-\tau))-\mathcal{D}(A(t)),$$
where $A(t)$ is the size of the adult population and $\mathcal{B}$ and $\mathcal{D}$ are the birth and death functions, respectively.

Let us deduce a stochastic counterpart of this model starting from the McKendrik-von Foerster equation (2). Assume that
$$m(t,a)=\begin{cases}\mu_J(t), & 0\le a<\tau,\\ \mu_A(A(t)), & a\ge\tau,\end{cases}$$
and the birth rate is given by
$$\beta(t,a)=\begin{cases}0, & 0\le a<\tau,\\ \beta_A(A(t)), & a\ge\tau,\end{cases}\tag{6}$$
where $\beta_A(A)$, $A\in(-\infty,\infty)$, is a continuously differentiable function, which satisfies the assumption $\beta_A'(A)<0$ for $A\ge 0$.

The coefficient γ in (A4) is a function of t, so that $\nu(t)=\int\limits_0^t\gamma(s)\,dB(s)$, and satisfies the condition $\gamma(t)\ge m>0$. Then we get
$$dA(t)=-\mu_A(A(t))A(t)\,dt+\alpha(t,\tau)\beta_A(A(t-\tau))A(t-\tau)\,dt+\gamma(t)A(t)\,dB(t),$$
for $t\ge\tau$, where
$$\alpha(t,\tau)=\exp\bigg\{-\int\limits_{t-\tau}^{t}\mu_J(s)\,ds+\nu(t)-\nu(t-\tau)-\frac{1}{2}\int\limits_{t-\tau}^{t}\gamma^2(s)\,ds\bigg\}.\tag{7}$$

Example 2: the stochastic counterpart of Nicholson's blowflies model.
The most celebrated model of the deterministic population dynamics is Nicholson's blowflies model and its generalizations (see, e.g., the review paper [1] and the references therein)
$$A'(t)=-m_AA(t)+p_0A(t-\tau)\exp\big\{-\theta A(t)\big\}.$$

Consider Eq. (5) for the adult population with the mortality rate $m(t,a)$ and the birth rate $\beta(t,a)$ given by (4) and (6), respectively. Assume also that $\gamma=\gamma(t)\ge m>0$. Then we get the following stochastic version of the generalized Nicholson's blowflies delay equation:
$$dA(t)=-m_AA(t)\,dt+\alpha(t,\tau)\beta_A(A(t-\tau))A(t-\tau)\,dt+\gamma A(t)A(t)\,dB(t),\tag{8}$$
where $\alpha(t,\tau)$ is given by (7). Notice that this equation differs from that studied in [7], where an additive stochastic noise was appended to the deterministic blowflies model:
$$dA(t)=-m_AA(t)\,dt+p_0A(t-\tau)\exp\big\{-\theta A(t-\tau)\big\}\,dt+\delta A(t)\,dB(t).\tag{9}$$

The main difference between Eq. (9), obtained by automatically adding a stochastic noise, and Eq. (8) obtained from the stochastic McKendrik-von Foester model (2) is the presence of the stochastic process $\alpha(t,\tau)$, which represents an intrinsic multiplicative stochastic noise. This random coefficient depends explicitly on the noise $\gamma\dot{B}$, which we added to the mortality rate in (2), and explains how random fluctuations in the population's mortality influence fluctuations in the birth function. This dependence is disregarded in Eq. (9). Note that as long as the noise $\gamma\dot{B}$ is non-zero, we will always get a nontrivial random α in front of the deterministic birth function β_A.

In addition, starting with (2) will always produce a random initial condition $A(t)=\varphi_A(t)$, $0\le t\le\tau$, as it was shown in the previous section.

References

[1] L. Berezansky, E Braverman and L. Idels, Nicholson's blowflies differential equations revisited: main results and open problems. *Appl. Math. Model.* **34** (2010), no. 6, 1405–1417.

[2] J. M. Cushing, Nonlinearity and stochasticity in population dynamics. *Mathematics for ecology and environmental sciences*, 125–144, Biol. Med. Phys. Biomed. Eng., *Springer, Berlin*, 2007.

[3] H. I. Freedman and K. Gopalsamy, Global stability in time-delayed single-species dynamics. *Bull. Math. Biol.* **48** (1986), no. 5-6, 485–492.

[4] M. E. Gurtin and R. C. MacCamy, Non-linear age-dependent population dynamics. *Arch. Rational Mech. Anal.* **54** (1974), 281–300.

[5] A. Ponosov, L. Idels and R. Kadiev, Stochastic McKendrick-von Foerster models with applications. *Phys. A* **537** (2020), 122641, 14 pp.

[6] S. L. Robertson, S. M. Henson, T. Robertson and J. M. Cushing, A matter of maturity: To delay or not to delay? Continuous-time compartmental models of structured populations in the literature 2000-2016. *Nat. Resour. Model.* **31** (2018), no. 1, e12160, 26 pp.

[7] W. Wang, L. Wang and W. Chen, Stochastic Nicholson's blowflies delayed differential equations. *Appl. Math. Lett.* **87** (2019), 20–26.