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Stochastic McKendrick-Von Foerster models with applications

Arcady Ponosov^{a,*}, Lev Idels^b, Ramazan Kadiev^c

^a Department of Sciences and Technology, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

^b Department of Mathematics, Vancouver Island University, 900 Fifth St. Nanaimo, BC, V9S5S5, Canada

^c Dagestan Research Center of the Russian Academy of Sciences & Department of Mathematics, Dagestan State

University, Makhachkala 367005, Russia

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ABSTRACT

A newly presented McKendrick–Von Foerster model with a stochastically perturbed mortality rate is examined. A transformation method converting the model with nonlocal boundary conditions into a system of stochastic functional differential equations is offered. The method could be viewed as analogous to the one which is widely used for such type of deterministic problems. The derived stochastic functional differential equations yield multiple classic population models with 'naturally born' stochasticity, including delayed Nicholson's blowflies, general recruitment and models with cannibalism, which by itself could be objects of future analysis and applications.

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1. Introduction

The most celebrated deterministic McKendrick–Von Foerster (DMF) model, which is widely used to examine agestructured populations, could be expressed as (see, for example, [1,2] or [3])

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -m(t, a)u \quad (t, a \ge 0)$$

with the initial condition

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

and the non-local boundary condition

$$u(t,0)=b(t)=\int_0^\infty \beta(t,a)u(t,a)da\geq 0.$$

Here u(t, a) is the size (density) of a certain population of a given age $a \ge 0$ at time $t \ge 0$, $m(t, a) \ge 0$ 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 $\beta(t, a)$. The variables are supposed to be continuous counterparts (statistical averages) of the integer-valued population sizes.

The DMF equation (1) is a balance equation that can be derived from the basic ('first') biophysical principles, by letting the increments in time and age be infinitely small and under the assumption that the population is closed to migration. The

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^{*} Corresponding author.

E-mail addresses: arkadi@nmbu.no (A. Ponosov), lev.idels@viu.ca (L. Idels), kadiev_r@mail.ru (R. Kadiev).

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equation can be, therefore, interpreted as a kind of a general 'conservation law'. That is why, it is widely used, in addition to classic population dynamics, in many fields of mathematical biology, e.g. in plant evolution, cell biology, biochemistry, but also in other areas like geophysics [4].

If the birth function b(t) is known, then the solution of (1) is easily obtained by integration along characteristics [3,5]. Otherwise, the DMF equation is used as a starting point to derive specific population models that can be treated in a more efficient manner. As a rule, this requires some simplifying assumptions on μ and β .

The most important determinant of population dynamics is the notion of the mortality rate. There is no shortage of variants of mortality rates in various areas of population dynamics. They can be both time- and age dependent [6], they can also depend on the total size (density) of the population, as e.g. in [7]:

$$m(t, a) = \left(\alpha_1(t, a) + \alpha_2(t, a) \int_0^\infty u(t, s) ds\right) u(t, a),$$

or on the sizes (densities) of the juvenile and adult populations [3].

If the mortality rate is autonomous, then the deterministic model (1) can be transformed into a classic Volterra integral equation or, by using other special methods, to a first-order delay differential equation.

Taking into account stochastic effects is very important part of any realistic population dynamics modeling approach. Demographic and environmental stochasticity arises from variation over time in factors external to a system and influence the survival of individuals in a population [8,9]. To mitigate this, it is common to include a random term in the equation governing the dynamics as a proxy for unmodeled variability. Natural systems are, almost by definition, heterogeneous. Thus, mortality rates are notoriously difficult to estimate, moreover, in ecological communities mortality rates are as diverse as populations; e.g. for trees they are often constants, for fishes they decrease for smaller fish and increase for larger species; for mammals they are often increasing and unbounded. There are several transitions between random and deterministic models, and the reason for this is the level at which we view the system. A widely used recipe to incorporate stochasticity into a model is a simple addition:

$$\mathfrak{T} u = \mathfrak{D} u + \mathfrak{S} u \tag{2}$$

where \mathfrak{D} and \mathfrak{S} stand for deterministic and stochastic components of the model, respectively. In most publications, one adds the noise to a simplified deterministic model, i.e. the one already derived from (1). In this case, stochasticity can be interpreted as an external noise or uncertainty in measurements. Typical examples can be found in [10] or [11], where the stochastic term is added to deterministic delay equations.

Another approach consists in adding intrinsic and extrinsic stochasticity to biologically meaningful variables, first of all to the mortality term in the DMF equation (1). This approach was used in the papers [12–15], where multiple options were offered. The most popular choice was the normal distribution and the associated Brownian motion or the Brownian sheet [12,13]. To model jumps in mortality, describing losses of population due to external events, the Poisson process was adopted in [14]. More complicated noises can be found in [16], where combinations of the Brownian motion and the Poisson process are studied, and in [15], where the fractional Brownian motion was added to DMF. Non-Gaussian (bounded) noises are treated in [17].

In this paper, we follow the latter approach and incorporate a general additive stochastic noise into the mortality rate function by the formula

$$\mu(t, a) = m(t, a) + \dot{\nu}(t),$$

where the locally Lebesgue integrable function m(t, a) denotes the deterministic term, while the random noise $\dot{v}(t)$ is the formal (generalized) derivative of the scalar stochastic process v(t). Intending to cover a widest possible variety of cases, we assume v(t) to be a semimartingale, continuous or discontinuous, as this is, in some sense, the most general stochastic integrator [18,19]. This leads to the following stochastic version of model (1):

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -(m(t, a) + \dot{\nu}(t))u \quad (t, a \ge 0).$$
(3)

As in the review paper [3], we treat the mortality rate m(t, a) and the birth rate $\beta(t, a)$, as well as the noise $\dot{\nu}(t)$ in the above stochastic McKendrick-von Foerster equation (SMF), as the functions depending on the aggregated age variables, i.e. on the total size of the juveniles J(t) and the adults A(t):

$$J(t) = \int_0^\tau u(t, a) da \quad \text{and} \quad A(t) = \int_\tau^\infty u(t, a) da,$$
(4)

where $\tau \ge 0$ is the maturation time. More precisely, we assume that $m = m_J$, $\beta = 0$ for $a \le \tau$ and $m = m_A$, $\beta = b_A$ for $a > \tau$, where m_J , m_A , β_A are functions of t, J(t), A(t), and the noise $\dot{\nu}$ is defined as $\dot{\nu}(t) = \gamma(t, J(t), A(t))\dot{Z}(t)$, where Z is another semimartingale which is independent of J and A.

The new model (3) embeds, within itself, a variety of the known stochastic age-distributed population dynamics. Whereas the deterministic conservation law (1) or its stochastic analog (3) are convenient formulations in population dynamics, both are less suitable for investigating qualitative properties of the solutions. The infinite dimensionality of the problem makes solving it a hard task. In contrast, there exists a highly developed qualitative theory of stochastic

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(5)

functional differential (SFD) equations [20–23] and [24], the recent advances in which inspired us to address the following question: how the stochastic partial differential equation (3) can be converted into a system of SFD equations? To the best of our knowledge, transformation of the McKendrick–Von Foerster equation into a simpler system of finite dimensional differential equations, with or without delays, is the groundwork for understanding and studying dynamical descriptions of biological processes. It seems that this idea has not been explored in the stochastic case, although it has been proven to be very fruitful in the deterministic case (see e.g. [3,5,25] and the references therein).

We stress that our objective is to simplify the SMF equation (3) by converting it to a SFD system. That is why, our framework does not require interpreting SMF as an abstract linear equation in a Banach space, as e.g. in [13,16] or [15]. Moreover, our model is highly nonlinear, both in the coefficients and the noise, and hence less suitable for trying methods based on infinite dimensional spaces or generalized derivatives.

The paper is organized as follows. In Section 2, an integral representation of solutions of the SMF equation driven by an arbitrary semimartingale is obtained. The representation is based on the so-called Doléans–Dade exponentials. In the next section, these formulae are used to derive SFD equations for the aggregated number of juveniles and adults defined in (4). More precisely, the obtained equations can be described as stochastic equations with both concentrated and distributed delays, random coefficients and random initial conditions.

In Section 4, we illustrate how the new SFD equations yield multiple classic population models with naturally introduced stochasticity. We show that deriving a specific population model from SMF (3) does not amount to simply adding a stochastic term to the analogous deterministic model that was derived from DMF (1). Indeed, fluctuations in the mortality rate must influence the production rate and, thus, stochasticity should enter the deterministic model in a non-additive way. Our calculations explain how it should be done rigorously. In particular, we obtain a new stochastic version of the celebrated Nicholson's blowflies equation.

Some open problems are mentioned in Section 5, while in Appendix we offer a proof of the main representation formula for the solutions of SMF (3).

2. Alternative formulation of the SMF equation

The definitions and the results from stochastic calculus used in this section can be found in e.g. [18] and [19]. The stochastic processes below are assumed to be defined on the filtered probability space

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

with the probability measure **P** on the σ -algebra \mathcal{F} of subsets of Ω and an increasing, right-continuous sequence of σ -subalgebras \mathcal{F}_t of \mathcal{F} , where all the introduced σ -algebras are complete with respect to the measure **P**. The expectation on this probability space is denoted by **E**.

Let \mathcal{B} be the σ -algebra of all Borel subsets of the interval $[0, \infty)$. Below we use

(a) \mathcal{F}_t -adapted stochastic processes $v(t) = v(t, \omega), t \in [0, \infty), \omega \in \Omega$, which means that $v(\cdot, \cdot)$ is $\mathcal{B} \otimes \mathcal{F}$ -measurable and the random variable $v(t, \cdot)$ is \mathcal{F}_t -measurable for each $t \in [0, \infty)$;

(b) càdlàg functions (from French: 'continue à droite, limite à gauche', which means 'right-continuous with left limits') and càdlàg stochastic processes, whose trajectories are almost surely càdlàg;

(c) the \mathcal{F}_t -adapted stochastic process $v(t) = v(t, \omega)$ (v(0) = 0), which is supposed to be a scalar semimartingale on the above filtered probability space, i.e. it belongs to the class of stochastic processes, with respect to which one can define stochastic integrals with 'reasonable' properties (the celebrated Bichteler–Dellacherie–Meyer–Mokobodzky theorem).

Remark 1. The stochastic process v(t) is used in this paper to incorporate the noise $\dot{v}(t)$ into the mortality rate. It is well-known that semimartingales are càdlàg stochastic processes. An important example of a continuous v(t) is given by the scalar Brownian motion, so that $\dot{v}(t)$ becomes the white noise. An example of a discontinuous v(t), which was studied in [14] in connection with SMF, is the Poisson process. More examples can be found in [18,19] and other books and papers.

The following assumption is valid throughout Section 2:

Assumption (A1). The filtered probability space (5) is kept fixed; the initial function $\chi(a) \ge 0$ is càdlàg for $a \ge 0$; the birth function $b(t) = b(t, \omega)$ is an \mathcal{F}_t -adapted, càdlàg stochastic process on $[0, \infty)$ and b(t) = 0 for t < 0; the mortality rate function $m(t, a) = m(t, a, \omega)$ is $\mathcal{B} \otimes \mathcal{B} \otimes \mathcal{F}$ -measurable, locally Lebesgue integrable in $t, a \ge 0$ for almost all ω, \mathcal{F}_t -adapted for almost all $a \ge 0$ and, in addition, m(t, a) = 0 outside the set $\{t, a \ge 0\}$; the stochastic process $v(t), t \ge 0$ is an arbitrary semimartingale satisfying the normalization condition v(0) = 0 and the estimate $\Delta v(t) > -1$ almost surely for all $t \ge 0$.

Remark 2. Assumption (A1) is formulated to cover the case of superpositions of Lipschitz functions with the \mathcal{F}_t -adapted, càdlàg stochastic processes J(t) and A(t), which will be solutions of certain SFD equations, see Section 3. The assumptions b(t) = 0 and m(t, a) = 0 outside the set $\{t, a \ge 0\}$ are technical: the positivity of solutions J(t) and A(t) may require additional assumptions, which are not considered in this paper. The assumption on the jumps of v is needed to ensure positivity of the solution u(t, a), see the representation formula (10) below.

Eq. (3) is interpreted in this paper as the integral equation

$$\int_{0}^{u} (u(t,s) - u(0,s))ds + \int_{0}^{t} (u(\sigma,a) - u(\sigma,0))d\sigma$$

$$= -\int_{0}^{t} \left(\int_{0}^{a} m(\sigma,s)u(\sigma,s)ds \right) d\sigma + \int_{0}^{t} \left(\int_{0}^{a} u(\sigma-s)ds \right) d\nu(\sigma)$$
(6)

(7)

supplied with the conditions

$$u(0, a) = \chi(a) \ (a \ge 0) \ \text{and} \ u(t, 0) = b(t) \ (t \ge 0),$$

where *m*, *b*, ν and χ satisfy assumption (A1).

Definition 1. A solution $u(t, a) = u(t, a, \omega)$ of SMF (3) $(t, a \in [0, \infty), \omega \in \Omega)$ is a positive, $\mathcal{B} \otimes \mathcal{B} \otimes \mathcal{F}$ -measurable function, such that the stochastic process $u(\cdot, a)$ is \mathcal{F}_t -adapted and càdlàg for all $a \ge 0$ and almost surely satisfies the integral equation (6) for $t, a \in [0, \infty)$.

Remark 3. It is quite essential for the forthcoming analysis that we treat SMF (3) as the integral equation (6) and thus avoid using generalized derivatives as well as any version of the so-called 'Stratonovich calculus' (see e.g. [26]), which is more restrictive than the classic Itô calculus. In our setting, the requirements from [26], upon which the Stratonovich calculus is based, are not fulfilled, as we operate with stochastic delay equations with random coefficients. But even in the case of non-delay equations, the Stratonovich calculus requires more conditions than the Itô calculus if driving semimartingales are discontinuous. However, these conditions are not always properly checked, especially in applications-oriented papers like [14], where the discontinuous Poisson noise is treated.

We also point out that integration with respect to both variables t and a is necessary in (6). Indeed, it follows from formulae (10) that the solutions are discontinuous in both variables, so that calculations based on generalized derivatives may lead to difficulties.

The a priori restrictions on u in Definition 1 seem to be appropriate as well. First of all, one has to integrate u with respect to v(t). Notice therefore that the stochastic process $u(t-, a) = \lim_{\sigma \to t^-} u(\sigma, a)$ on the right-hand side of Eq. (6) is well-defined if $u(\cdot, a)$ is càdlàg, and integrable with respect to the semimartingale v(t) as $u(\cdot, a)$ is \mathcal{F}_t -adapted [18, p. 170]. On the other hand, the solution formulae (10) show that u is to be càdlàg for all $a \ge 0$.

Finally, we remark that one can use u(t, a) instead of u(t-, a) in the stochastic integral at times t where v(t) is continuous.

In the deterministic case, the substitutions $\xi = \pm (t - a)$ transform the DMF equation (1) into a system of ordinary differential equations, which can be integrated if b(t) is known. In the stochastic case, we first reduce Eq. (6) to an integral analog of DMF (1) and derive thereof the explicit formulae for the solutions of (6). To do it, we use the Doléans–Dade exponential $X(t) = \mathcal{E}{Y(t)}$, which by the definition is the solution of the linear problem dX(t) = X(t-)dY(t), X(0) = 1, driven by a semimartingale Y [18, p. 202]. If Y(t) is continuous, then

$$\mathcal{E}\{Y(t)\} = \exp\{Y(t) - \frac{1}{2}[Y](t)\},\$$

where [Y](t), defined by

$$[Y](t) = \lim_{\|P\| \to 0} \sum_{k=1}^{n} (Y(t_k) - Y(t_{k-1}))^2, \quad \|P\| = \max_k (t_k - t_{k-1}), \tag{8}$$

is the quadratic variation of the stochastic process Y(t) and $P = \{t_k\}$ ranges over all possible partitions of the interval [0, t].

If Y is an arbitrary, i.e. not necessarily continuous, semimartingale, then [18,19]

$$\mathcal{E}\{Y(t)\} = \exp\{Y(t) - \frac{1}{2}[Y](t)\} \prod_{s \le t} (1 + \Delta Y(s)) \exp\{-\Delta Y(s) + \frac{1}{2} \Delta Y^{2}(s)\}$$

$$= \exp\{Y(t) - \frac{1}{2}[Y]^{c}(t)\} \prod_{s \le t} \exp\{-\Delta Y(s)(1 + \Delta Y(s))\},$$
(9)

where the number of jumps $\Delta Y(s) = \Delta Y(s, \omega)$ is countable for almost all $\omega \in \Omega$ and $[Y]^c(t) = [Y](t) - \sum_{s \le t} \Delta Y^2(t)$ is the continuous part of the quadratic variation of Y(t).

The following property of the Doléans–Dade exponentials is straightforward: $X(t) = \mathcal{E}{Y(t)} > 0$ for all $t \ge 0$ iff all jumps of the process Y(t) almost surely satisfy $\Delta Y(t) > -1$.

We claim that under assumption (A1), the solution of Eq. (6), satisfying conditions (7), is given by

$$u(t,a) = \begin{cases} \chi(a-t)\exp\{-\int_0^t m(s,a-t+s)ds\}\mathcal{E}\{\nu(t)\}, & t \le a, \\ b(t-a)\exp\{-\int_0^a m(t-a+s,s)ds\}\mathcal{E}\{\nu(t)\}\mathcal{E}^{-1}\{\nu(t-a)\}, & t > a. \end{cases}$$
(10)

Remark 4. The assumption $\Delta v(t) > -1$ ensures positivity of the solution u(t, a), which is essential as the latter describes the size of a population. On the other hand, this assumption guarantees invertibility of the Doléans–Dade exponential $\mathcal{E}{v(t-a)}$.

If v(t) is continuous, i.e. if $\Delta v(t) = 0$ for all $t \ge 0$, then (10) becomes

$$u(t, a) = \begin{cases} \chi(a-t) \exp\{-\int_0^t m(s, a-t+s)ds + \nu(t) - \frac{1}{2}[\nu](t)\}, \\ b(t-a) \exp\{-\int_0^a m(t-a+s, s)ds + \nu(t) - \nu(t-a) - \frac{1}{2}[\nu](t) + \frac{1}{2}[\nu](t-a)\} \end{cases}$$
(11)

for $t \leq a$ and t > a, respectively.

Representation (10) is proven in Appendix.

3. Transformation of SMF into a system of stochastic functional differential equations

In this section, we show how to derive equations for the aggregated age functions J(t) and A(t), defined in (4), from SMF (3). Our calculations presuppose that there exists a solution u(t, s) of (3) satisfying the conditions

$$u(0, a) = \chi(a) \qquad u(t, 0) = b(t) = \int_0^\infty \beta(t, a)u(t, a)da.$$
(12)

The precise hypotheses put on the birth rate β , the mortality rate *m*, the initial function ξ and the stochastic noise ν are described in assumptions (A2)-(A5) below.

Definition 2. A real-valued (deterministic) function $\alpha(t, x, y)$, $t \ge 0, x, y \in (-\infty, \infty)$ 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:

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

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

The following will be assumed throughout this section:

(A2). The mortality rate m(t, a) is defined as

$$m(t, a) = \begin{cases} m_J(t) \coloneqq \mu_J(t, J(t), A(t)), & 0 \le a < \tau, \\ m_A(t) \coloneqq \mu_A(t, J(t), A(t)), & a \ge \tau, \end{cases}$$
(13)

where μ_1 and μ_A are class L functions (that is, they are independent of the age *a*) and $\tau \ge 0$ is the maturation time.

(A3). The function $\chi(a) \ge 0$ (the initial age distribution at time t = 0) is càdlàg and satisfies the condition $\int_0^\infty \sup_{s\ge a} \chi(s) da < \infty$. In practical applications, the function χ has a compact support, so that this assumption will be trivially satisfied.

(A4). At any time *t*, the birth rate function β is defined as

$$\beta(t, a) = \begin{cases} 0, & 0 \le a < \tau, \\ \beta_A(t) := \beta_A(t, J(t), A(t)), & a \ge \tau, \end{cases}$$
(14)

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.

Similar assumptions can be found in [3] for the case of the DMF equation (1).

Notice that the second condition in (7) and (A4) imply the equality

$$b(t) = u(t, 0) = \beta_A(t)A(t).$$
 (15)

In addition, we require that

(A5). The semimartingale v is defined as

$$\nu(t) = \int_0^t \gamma(s, J(s-), A(s-)) dZ(s),$$
(16)

where a class L function γ satisfies the estimates $-\gamma_1 < \gamma(t, y_1, y_2) < \gamma_2$ ($t \ge 0, \infty < y_1, y_2 < \infty$) for some $0 \le \gamma_i \le \infty$ and Z(t) is a semimartingale on the filtered probability space (5), for which

$$\gamma_1^{-1} \ge \Delta Z(t) \ge -\gamma_2^{-1} \quad \text{almost surely for all } t \ge 0.$$
(17)

Remark 5. From the formal point of view, there is no difference between the semimartingales ν and Z, but this change of notation, together with assumptions (A2) and (A4), will give us stochastic equations where the stochastic noise depends on the solutions.

Inequality (17) guarantees that the condition $\Delta v(t) > -1$ is almost surely fulfilled for all $t \ge 0$. This implies positivity of the Doléans–Dade exponential $\mathcal{E}{v(t)}$ (and thus of the population size u(t, a)). This ensures also global existence of solutions of the equations for the aggregated variables J and A.

If Z is continuous, then $\gamma_1 = \gamma_2$ can be chosen to equal ∞ , so that no additional assumptions on $\gamma(t, y_1, y_2)$ are required.

According to (10), the function $u(\cdot, a)$ is \mathcal{F}_t -adapted for all a. It is therefore straightforward to check that also J(t) and A(t), and therefore $m_J(t)$, $m_A(t)$, $\beta_A(t)$, are all \mathcal{F}_t -adapted stochastic processes, provided that the integral for A(t) converges (for this property, see (23)).

To derive a stochastic delay equation for the variable J(t) (juveniles), let us put $a = \tau$ in (6). Then

$$\int_{0}^{t} (u(t,s) - u(0,s))ds + \int_{0}^{t} (u(\sigma,\tau) - u(\sigma,0))d\sigma$$
(18)

$$= -\int_0^t \left(\int_0^{\sigma} m(\sigma, s) u(\sigma, s) ds \right) d\sigma + \int_0^t \left(\int_0^a u(\sigma - s) ds \right) d\nu(\sigma).$$

Minding (4), (13) and (15), we arrive at

$$J(t) - J(0) + \int_0^t \left(u(\sigma, \tau) - \beta_A(\sigma) A(\sigma) \right) d\sigma = -\int_0^t m_J(\sigma) J(\sigma) d\sigma + \int_0^t J(\sigma) d\nu(\sigma),$$
(19)

as $0 \le s \le \tau$. To calculate $u(\sigma, \tau)$, we use the assumption $a \le \tau$, the second formula in (10) and again the formulae (13) and (15). Then for $t \ge \tau$

$$u(t,\tau) = \beta(t-\tau)A(t-\tau)\exp\{-\int_{t-\tau}^{t} m_{J}(s)ds\}\mathcal{E}\{\nu(t)\}\mathcal{E}^{-1}\{\nu(t-\tau)\},$$
(20)

as $\int_0^{\tau} m(t-\tau+s,s)ds = \int_0^{\tau} m_J(t-\tau+s)ds = \int_{t-\tau}^{t} m_J(s)ds$ if $0 \le s \le \tau$. Summarizing the above calculations, the following stochastic functional differential equation for the variable J(t) is obtained:

$$dJ(t) = \beta_A(t, J(t), A(t))A(t)dt - \mu_J(t, J(t), A(t))J(t)dt$$

- $\mathcal{D}\{t, J(\cdot), A(\cdot), X(\cdot)\}\beta_A(t - \tau, J(t - \tau), A(t - \tau))A(t - \tau)dt$
+ $\gamma(t, A(t -), J(t -))J(t -)dZ(t) \quad (t \ge \tau),$ (21)

where $X(t) = \mathcal{E}{v(t)}$ and

$$\mathcal{D}\{t, J(\cdot), A(\cdot), X(\cdot)\} = \exp\{-\int_{t-\tau}^{t} \mu_J(s, J(s), A(s))ds\}X(t)X^{-1}(t-\tau)$$
(22)

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

The derivation of the equation for the variable A(t) is more involved, as it includes improper integrals. To this end, we check that for each $t \ge 0$

$$\lim_{a_1,a_2\to\infty} \mathbf{E}\left(\int_{a_1}^{a_2} u(t,a)da\right)^2 = 0,$$
(23)

$$\lim_{a \to \infty} \mathbf{E} \left(\int_0^t u(\sigma, a) d\sigma \right)^2 = 0, \tag{24}$$

$$\lim_{a \to \infty} \mathbf{E} \left(\int_0^t m_A(\sigma) d\sigma \int_a^\infty u(\sigma, s) ds \right)^2 = 0,$$
(25)

and

$$\lim_{a \to \infty} \mathbf{E} \left(\int_0^t d\nu(\sigma) \int_a^\infty u(\sigma - s) ds \right)^2 = 0.$$
(26)

The property (23) ensures, in particular, that the integral (4) converges, so that the stochastic process A(t) in (4) is well-defined.

Denoting $\psi(a) = \sup_{s \ge a} \chi(a)$ and minding (A3) yield

$$\int_0^\infty \psi(a)da < \infty. \tag{27}$$

The following estimate for stochastic integrals is used below:

$$\mathbf{E}\left(\int_{0}^{t} v(\sigma)dv(\sigma)\right)^{2} \leq C(t)\mathbf{E}\left(\int_{0}^{t} v^{2}(\sigma)d\lambda(\sigma)\right).$$
(28)

It holds for a certain almost surely increasing stochastic process $\lambda(\sigma)$, a positive deterministic function C(t) and any predictable stochastic process $v(\sigma)$ [18,19].

Taking into the account inequality (28) and putting $\theta(t) = \int_0^t m_A(s) ds$, $\theta(t) = \lambda(t)$ in the case of (25) and (26), respectively, yield

$$\mathbf{E}\left(\int_0^t d\theta(\sigma) \int_a^\infty u(\sigma - s) ds\right)^2 = \\ \mathbf{E}\left(\int_0^t \varepsilon\{\nu(\sigma - s)\} \exp\{-\int_0^\sigma m_A(\xi) d\xi\} \int_a^\infty \chi(s - \sigma + s) ds d\theta(\sigma)\right)^2$$

for $a > t + \tau$. As

$$\sup_{0 \le \sigma \le t} \int_{a}^{\infty} \chi(s - \sigma +) ds = \sup_{0 \le \sigma \le t} \int_{a - \sigma}^{\infty} \chi(\eta +) d\eta \le \int_{a - t}^{\infty} \psi(\eta) d\eta$$

we obtain that

$$\lim_{a\to\infty} \mathbf{E}\left(\int_0^t d\theta(\sigma) \int_a^\infty u(\sigma,s) ds\right)^2 = 0.$$

This implies (25) with $m_A = \theta$ if we notice that $u(\sigma, a)$ can be replaced by $u(\sigma, a)$ under the integral. If $\theta = \lambda$, then

$$\lim_{a\to\infty} \mathbf{E}\left(\int_0^t d\lambda(\sigma) \int_a^\infty u(\sigma-s) ds\right)^2 = 0.$$

as u(t-, a) is predictable in t for each $a \ge 0$. This, together with (28), implies (26).

To derive the equation for the variable A(t), we first subtract (18) from (6)

$$\int_{\tau}^{u} (u(t,s) - u(0,s)) ds + \int_{0}^{t} (u(\sigma,a) - u(\sigma,\tau)) d\sigma$$

$$= -\int_0^t \left(\int_\tau^a m_A(\sigma) u(\sigma, s) ds \right) d\sigma + \int_0^t \left(\int_\tau^a u(\sigma, s) ds \right) d\nu(\sigma)$$

Letting $a \to \infty$ and utilizing properties (23)–(26) we arrive at

$$A(t) - A(0) - \int_0^t u(\sigma, \tau) d\sigma = -\int_0^t m_A(\sigma) A(\sigma) d\sigma + \int_0^t A(\sigma) d\nu(\sigma).$$
(29)

According to (10) and (13),

$$u(t,\tau) = b(t-\tau)\mathcal{E}\{v(t)\}\mathcal{E}^{-1}\{v(t-\tau)\}\exp\{-\int_0^{\tau} m_J(t-\tau+s)ds\} \ (t \ge \tau)$$

From (29), using assumptions (A2), (A4), (A5) and equality (15), we obtain the following stochastic functional differential equation:

$$dA(t) = -\mu_A(t, J(t), A(t))A(t)dt +$$

$$\mathcal{D}\{t, J(\cdot), A(\cdot), X(t)\}\beta_A(t, J(t-\tau), A(t-\tau))A(t-\tau)dt +$$

$$\gamma(t, J(t-), A(t-))A(t-)dZ(t) \quad (t \ge \tau),$$
(30)

where $X(t) = \mathcal{E}{v(t)}$ and the integral operator \mathcal{D} is defined in (22).

The system of Eqs. (21) and (30) should be supplied by the third equation for the auxiliary variable $X(t) = \mathcal{E}\{v(t)\}$. From assumption (A5) and the definition of the Doléans-Dade exponentials we obtain

$$dX(t) = \gamma(t, J(t-), A(t-))X(t-)dZ(t).$$
(31)

Notice that if the stochastic noise is not present, i.e. if $\dot{\eta} = \gamma \dot{Z} = 0$, then Eqs. (21) and (30) coincide with their deterministic counterparts (22)-(23) in [3] (up to slight notational changes).

Remark 6. Note that if the semimartingale Z has continuous trajectories, e.g. if Z is the Brownian motion, then we can

write J(t) and A(t) instead of the left-side limits J(t-) and A(t-) in Eqs. (21) and (30), respectively. If we ignore the maturation period and set $\tau = 0$, then J(t) = 0 and $A(t) = \int_0^\infty u(t, a)da$, and we obtain the ordinary stochastic differential equation with non-random coefficients with respect to A(t):

$$dA(t) = -\mu_A(t, J(t), A(t))A(t)dt + \beta_A(t, J(t), A(t))A(t)dt + \gamma(t, J(t-), A(t-))A(t-)dZ(t),$$
(32)

where $t \ge 0$. Indeed, in this case

$$\exp\{-\int_{t-\tau}^{t} \mu_{J}(s, J(s), A(s))ds\} \mathcal{E}\{\nu(t)\} \mathcal{E}^{-1}\{\nu(t-\tau)\} dt$$

=
$$\exp\{-\int_{t-\tau}^{t} \mu_{A}(s, J(s), A(s))ds\} \mathcal{E}\{\nu(t)\} \mathcal{E}^{-1}\{\nu(t-\tau)\} dt$$

= 1.

The system of functional differential equations (21), (30) and (31) should be supplied by the initial conditions

$$J(t) = \varphi_J(t), \quad A(t) = \varphi_A(t) \text{ and } X(t) = \varphi_X(t) \quad (t \in [0, \tau]),$$
(33)

where $\varphi_l(\cdot)$, $\varphi_A(\cdot)$ and $\varphi_X(t)$ are \mathcal{F}_{τ} -measurable, càdlàg stochastic processes.

In order to explain randomness in the initial data $\varphi_I(t)$, $\varphi_A(t)$ and $\varphi_X(t)$, let us go back to Eqs. (19) and (29) and assume that $0 \le t \le \tau$. In this case, the term $u(t, \tau)$ must be calculated according to the first formula in the solution (10), i.e.

$$u(t,\tau) = \chi(\tau-t) \exp\{-\int_0^t m(s,\tau-t+s)ds\} \mathcal{E}\{\nu(t)\} = \chi(\tau-t) \exp\{-\int_0^t m_J(s)ds\} \mathcal{E}\{\nu(t)\}$$
(34)

due to the definition (13) of the mortality rate and the observation that $\tau - t + s \le \tau$ if $0 \le s \le t$. Therefore, we obtain the following system of stochastic integro-differential equations on the interval $[0, \tau]$:

$$dJ(t) = -\mathcal{D}\{t, J(\cdot), A(\cdot)\}dt + \beta_A(t, J(t), A(t))A(t)dt - \mu_J(t, J(t), A(t))J(t)dt + \gamma(t, A(t-), J(t-))J(t-)dZ(t) dA(t) = \mathcal{D}\{t, J(\cdot), A(\cdot)\}dt - \mu_A(t, J(t), A(t))A(t)dt + \gamma(t, J(t-), A(t-))A(t-)dZ(t) dX(t) = \gamma(t, J(t-), A(t-))X(t-)dZ(t),$$
(35)

where

$$\mathcal{D}_{0}\{t, J(\cdot), A(\cdot), X(\cdot)\} = \chi(\tau - t) \exp\{-\int_{0}^{t} \mu_{J}(s, J(s), A(s))ds\}X(t),$$
(36)

and the initial conditions are given by

$$J(0) = \int_{\tau}^{\infty} u(0, s) ds = \int_{\tau}^{0} \chi(s) ds,$$

$$A(0) = \int_{\tau}^{\infty} u(0, s) ds = \int_{\tau}^{\infty} \chi(s) ds,$$

$$X(0) = 1.$$
(37)

This is a particular case of a stochastic hereditary equation, sometimes called Doléans–Dade and Protter's equation, see e.g. [27]. According to the results from [27], the initial value problem (35)–(37) has a unique (up to the natural equivalence of stochastic processes) solution ($\varphi_J(t)$, $\varphi_A(t)$, $\varphi_X(t)$) for $t \in [0, \tau]$. This solution is \mathcal{F}_{τ} -measurable and càdlàg. This justifies our assumptions in (33).

4. Some specific stochastic models derived from the SMF equation

In this section we present a natural algorithm to justify stochastic versions of some classic deterministic models for a single age-structured population. As we mentioned in the introduction, the most widespread way to incorporate stochasticity into a deterministic model is to append an additive noise term. In our setting, we add the stochastic noise to the basic age-structured population model (1) resulting in SMF (3). Taking this equation as a starting point, we show what kind of SFD one should expect to obtain. In most cases, the stochasticity would appear simultaneously as an additive and multiplicative noise in the equation and, in addition, in the initial conditions. Thus, our approach leads to equations that are very different from those one can derive by appending an additive stochasticity to a model derived from the deterministic McKendrick–Von Foerster equation. Complexity of the new models obtained by our algorithm would, therefore, require more than just the well-elaborated techniques. For instance, stability analysis, which in most cases is heavily based on the classical Lyapunov functions framework, may be less suitable in our case.

In the first two examples, we only use Eq. (30) for adults. In order to disengage this equation from Eq. (21) for juveniles, one should basically assume that the functions in assumptions (A2), (A4) and (A5) are independent of the variable *J*, exactly as in the deterministic case [3].

4.1. The recruitment-delayed model

The following equation is widely used in population dynamics (see e.g. the monograph [28] or the review paper [29]):

$$A'(t) = \mathcal{B}(A(t-\tau)) - \mathcal{D}(A(t)), \tag{38}$$

where A(t) is the size of the adult population and \mathcal{B} and \mathcal{D} are the birth and death functions, respectively. Additive stochasticity terms would lead to stochastic equations of the following kind:

$$dA(t) = \mathcal{B}(A(t-\tau))dt - \mathcal{D}(A(t))dt + g(A(t))dZ(t).$$
(39)

Let us instead start from SMF (3). Assume that

$$m(t, a) = \begin{cases} \mu_J(t), & 0 \le a < \tau, \\ \mu_A(A(t)), & a \ge \tau, \end{cases}$$

$$(40)$$

and the birth rate is given by

$$\beta(t,a) = \begin{cases} 0, & 0 \le a < \tau, \\ \beta_A(A(t)), & a \ge \tau, \end{cases}$$

$$(41)$$

where $\beta_A(\cdot)$ is continuously differentiable on the real line and decreasing on the positive half-line.

Assume also that $\gamma = \gamma(A) > m > 0$ and all jumps of the semimartingale Z satisfy $\Delta Z(t) \ge -m^{-1}$. Then

$$dA(t) = -\mu_A(A(t))A(t)dt + \alpha(t,\tau)\beta_A(A(t-\tau))A(t-\tau)dt + \gamma(A(t-))A(t-)dZ(t)$$
(42)

for $t \geq \tau$ and

$$\alpha(t, A(\cdot)) = \exp\{-\int_{t-\tau}^t \mu_J(s)ds\} \mathcal{E}\{\gamma(A(t))Z(t)\} \mathcal{E}^{-1}\{\gamma(A(t-\tau))Z(t-\tau)\}.$$

Remark 7. The main difference between Eq. (39), obtained by automatically adding a stochastic noise, and Eq. (42) is the presence of the \mathcal{F}_t -adapted and càdlàg stochastic process $\alpha(t, \tau)$, which represents an intrinsic multiplicative stochastic noise. This random coefficient depends explicitly on the noise $\gamma \dot{Z}$, which we added to the mortality rate in SMF (3), and explains how random fluctuations in the population's mortality influence fluctuations in the birth function. Note that as long as the noise $\gamma \dot{Z}$ is non-zero, we will always get a nontrivial random α in front of the deterministic birth function β_A .

In addition, starting with SMF (3) 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.

4.2. Stochastic 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 [29] and references therein)

$$A'(t) = -m_A A(t) + p_0 A(t - \tau) \exp\{-\theta A(t)\}.$$
(43)

Note that this model was derived from DMF (1) in [30].

In [11], an additive stochastic noise was appended to Eq. (43):

$$dA(t) = -m_A A(t) dt + p_0 A(t-\tau) \exp\{-\theta A(t)\} dt + \delta A(t) dB(t), \quad t \ge 0,$$
(44)

where B(t) is the scalar Brownian motion and A(t) satisfies the deterministic initial condition $A(t) = \varphi(t)$ on $-\tau \le t \le 0$. Based on SMF (3), we obtain a new stochastic Nicholson-type model with random initial conditions. Consider Eq. (30) for the adult population with the following the piecewise mortality rate

$$m(t, a) = \begin{cases} m_J = \text{const}, & 0 \le a < \tau, \\ m_A = \text{const}, & a \ge \tau, \end{cases}$$
(45)

with the birth rate $\beta(t, a)$ given by (41). The coefficient γ in (A5) is a function of A, so that $\dot{v}(t) = \gamma(A(t)\dot{Z}(t))$, and satisfies the condition $\gamma(A) \ge m > 0$. Finally, assume that all jumps of the semimartingale Z satisfy $\Delta Z(t) > -m^{-1}$. Then we get the following stochastic version of the generalized Nicholson blowflies delay equation:

$$dA(t) = -m_A A(t) dt + \alpha(t, \tau) \beta_A (A(t-\tau)) A(t-\tau) dt + \gamma (A(t)) A(t-) dZ(t),$$
(46)

where

$$\alpha(t,\tau) = \exp\{-m_j\tau\} \mathcal{E}\{\gamma(A(t))Z(t)\} \mathcal{E}^{-1}\{\gamma(A(t-\tau))Z(t-\tau)\}$$
(47)

is an \mathcal{F}_t -adapted and càdlàg stochastic process.

Notice that if

$$\beta_A(A) = p_0 \exp\{-\theta A\} \quad (\theta > 0) \tag{48}$$

and Z = 0, then (46) simplifies to the deterministic blowflies equation (43). However, if the stochastic noise is nontrivial, we will always get random coefficients and random initial conditions, unlike the stochastic version of the Nicholson delay equation (44) studied in [11].

4.3. Stochastic models of cannibalism

After the publication of the seminal paper [31], the mathematical models of cannibalism based on differential equations became very popular in the literature (see e.g. the review paper [32] and the references therein). Not pretending to cover more sophisticated models, which take into account various aspects of cannibalism, we restrict ourselves to a comparatively simple version, which was studied in [33].

Let

$$m(t,a) = \begin{cases} d_1 + c_1 A(t), & 0 \le a < \tau, \\ d_2 - c_2 J(t), & a \ge \tau, \end{cases}$$
(49)

where the birth rate $\beta(t, a)$ is given by (41), and c_1, c_2, d_1 and d_2 are all positive constants. The choice of the mortality function in (49) implies that the death rate of juveniles increases along with the size of the adult population, since the mortality rate of adults due to cannibalism increases.

For the sake of simplicity, we assume that the function γ defined in (A5) is a positive constant, i.e. $\gamma = \gamma_0$ and all jumps of the semimartingale *Z* satisfy $\Delta Z(t) > -\gamma_0^{-1}$.

Then from (21), (30) and (31) we get the following system of SFD:

$$dJ(t) = (\beta_{A}(A(t))A(t) - d_{1}J(t) - c_{1}A(t)J(t)) dt - \mathcal{D}\{A(\cdot)\}\beta_{A}(A(t-\tau))A(t-\tau)dt + \gamma_{0}J(t-)dZ(t) dA(t) = (-d_{2}A(t) + c_{2}A(t)J(t)) dt + \mathcal{D}\{A(\cdot)\}\beta_{A}(A(t-\tau))A(t-\tau)dt + \gamma_{0}A(t-)dZ(t) \quad (t \ge \tau),$$
(50)

where

$$\mathcal{D}\{A(\cdot)\} = \exp\{-\int_{t-\tau}^{t} (d_1 + c_1 A(s)) ds\} \mathcal{E}\{\gamma_0 Z(t)\} \mathcal{E}^{-1}\{\gamma_0 Z(t-\tau)\}$$
(51)

is an integral operator standing for the distributed delay in the equation. If Z = 0 and $\beta_A(A)$ is given by (48), then the system (50) coincides with the system (3.2) in [33].

5. Conclusions and outlook

The McKendrick–Von Foerster equation for an age-structured population with a stochastically perturbed mortality rate function was examined. Based on this equation, a system of stochastic functional differential equations was derived for the aggregated variables describing the size of juveniles and adults in the population. We showed that adding a stochastic noise to the mortality rate would yield stochastic systems with both random coefficients and random initial functions, the latter deviate from the systems one mechanically obtains by appending an additive stochasticity to the well-known deterministic models.

Note that in our report we did not examine the case of the stochastically perturbed per capita birth rate function β . In fact, changes in our calculations would be minimal with the addition of a differentiable stochastic noise to β . However, such model would have limited applications, since neither white noise, nor Poisson noise would be covered. Including more general stochasticity in the model will require special tools and is, therefore, left for future studies.

In addition, we intend to pursue the following problems in the near future:

- (1) To justify the existence and uniqueness result for the SMF equation (3) equipped with conditions (12), which satisfy assumptions (A2)-(A5).
- (2) To find conditions, under which the solutions of system (21), (30) and (31), or at least, of the equations in Sections 4.1–4.3, will be positive.
- (3) Derive new delay stochastic models from the SMF, which contain multi-age classes and population groups or describe other types of interactions between them. Some examples are (to name only a few): more realistic cannibalism models (three age classes), models of marine protection areas (two groups and two age classes), stochastic predator-prey type models (two groups and two age classes), commensalism models [34].
- (4) Elaborate efficient analytic tools to study basic properties of SFD derived in Sections 2 and 4, especially those related to extinction, persistence, existence and stability of stationary regimes (which will be invariant measures rather than constants).

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Appendix

Below we offer a rigorous proof of the representation formulae (10).

Theorem 1. If assumption (A1) is fulfilled, then the solution of problem (6)–(7) is given by (10).

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To prove Theorem 1, we need some lemmas.

First of all, we will study existence of (not necessarily smooth) solutions to the integral version of the DMF equation (1) equipped with more general boundary conditions. This will give us an opportunity to reduce the SMF equation (3) to the DMF equation (1), both written in the integral form, via the substitution $\bar{u}(t, a) = u(t, a)\varepsilon^{-1}\{v(t)\}$. For the sake of simplicity, we use the notation u(t, a) for the solutions of DMF (1) in Lemma 1 below. In Theorem 1, where SMF (3) and DMF (1) are treated simultaneously, the solutions of these two equations will be denoted differently.

In Lemma 1, we check that the function

$$u(t, a) = \begin{cases} v_1(a-t) \exp\{-\int_0^t m(s, a-t+s)ds\}, & t \le a, \\ v_2(t-a) \exp\{-\int_0^a m(t-a+s, s)ds\}, & t > a, \end{cases}$$
(52)

satisfies the following integral version of DMF (1):

$$\int_0^a (u(t,s) - u(0,s))ds + \int_0^t (u(\sigma,a) - u(\sigma,0))d\sigma = -\int_0^t \left(\int_0^a m(\sigma,s)u(\sigma,s)ds\right)d\sigma$$
(53)

equipped with conditions (7), where the functions v_1 and v_2 replace the initial function χ and the birth function b, respectively, and are only assumed to be Lebesgue integrable on any bounded interval [0, T].

Remark 8. If v_1 and v_2 are smooth, then formulae (52) can be verified by a direct differentiation. In the non-smooth case, the corresponding result is justified in the lemma below.

Lemma 1. Let $v_1(y)$, $v_2(y)$ be Lebesgue integrable functions on an interval [0, T] and the function m(t, a) be Lebesgue integrable on $[0, T] \times [0, T]$. Then formulae (52) provide a solution to Eq. (53) on the set $0 \le t$, $a \le T$ satisfying the conditions $u(0, a) = v_1(a)$ and $u(t, 0) = v_2(t)$ for almost all $0 \le a \le T$ and $0 \le t \le T$, respectively.

Proof. Denote

$$p(t, a) = \begin{cases} \exp\{-\int_0^t m(s, a - t + s)ds\}, & t \le a, \\ \exp\{-\int_0^a m(t - a + s, s)ds\}, & t > a, \end{cases}$$
(54)

and

$$v(y) = \begin{cases} v_1(-y), & -T \le y < 0, \\ v_2(y), & 0 \le y \le T. \end{cases}$$
(55)

We have to check that

$$\int_{0}^{a} (p(t,s)v(t-s) - p(0,s)v(-s))ds + \int_{0}^{t} (p(\sigma,a)(v(\sigma-a) - p(\sigma,0)v(\sigma)))d\sigma = -\int_{0}^{t} \left(\int_{0}^{a} m(\sigma,s)p(\sigma,s)v(\sigma-s)ds\right)d\sigma$$
(56)

for $-T \le t$, $a \le T$. The substitutions in the four integrals on the left-hand side, defined as $\eta = t - s$, $\eta = -s$, $\eta = \sigma - a$ and $\eta = \sigma$, respectively, result in

$$\int_{t-a}^{t} p(t, t+\eta) v(\eta) d\eta - \int_{-a}^{0} p(0, -\eta) v(\eta) d\eta + \int_{-a}^{t-a} p(a+\eta, a) v(\eta) d\eta - \int_{0}^{t} p(\eta, 0) v(\eta) d\eta,$$
(57)

while the substitution $\eta = \sigma - s$ on the right-hand side yields

$$-\int_{0}^{t} \left(\int_{\sigma-a}^{\sigma} m(\sigma, \eta+\sigma) p(\sigma, \sigma-\eta) v(\eta) d\eta \right) d\sigma.$$
(58)

Now, we take an arbitrary $v \in L^1([-T, T])$ and find a sequence of smooth functions v_n , which converges to v in the L^1 -topology. This implies that v_n converges in the weak topology of the space L^1 , and in particular,

$$\begin{split} \int_{t-a}^{t} p(t,t+\eta)v_n(\eta)d\eta &\to \int_{t-a}^{t} p(t,t+\eta)v(\eta)d\eta, \\ \int_{-a}^{0} p(0,-\eta)v_n(\eta)d\eta &\to -\int_{-a}^{0} p(0,-\eta)v(\eta)d\eta \\ \int_{-a}^{t-a} p(a+\eta,a)v_n(\eta)d\eta &\to \int_{-a}^{t-a} p(a+\eta,a)v(\eta)d\eta, \\ \int_{0}^{t} p(\eta,0)v_n(\eta)d\eta &\to \int_{0}^{t} p(\eta,0)v(\eta)d\eta \end{split}$$

for all $0 \le a, t \le T$. On the other hand, the sequence of functions

$$V_n(\sigma) = \int_{\sigma}^{\sigma-a} m(\sigma, \eta + \sigma) p(\sigma, \sigma - \eta) v_n(\eta) d\eta$$

converges to the limit

$$\int_{\sigma-a}^{\sigma} m(\sigma, \eta+\sigma) p(\sigma, \sigma-\eta) v(\eta) d\eta$$

for all $\sigma > 0$, a > 0 and, in addition, $V_n(\sigma)$ satisfies the estimate

$$|V_n(\sigma)| \leq \max_{0 \leq t, a \leq T} \int_{\sigma-a}^{\sigma} |v_n(\eta)d\eta \leq \max_{0 \leq t, a \leq T} \int_{-T}^{T} |v_n(\eta)d\eta \leq C,$$

as the sequence $\{v_n\}$ converges in $L^1[-T, T]$. Thus, by the Lebesgue convergence theorem, the sequence

$$-\int_0^t \left(\int_{\sigma-a}^{\sigma} m(\sigma,\eta+\sigma)p(\sigma,\sigma-\eta)v_n(\eta)d\eta\right)d\sigma$$

converges to the limit

$$-\int_0^t \left(\int_{\sigma-a}^{\sigma} m(\sigma,\eta+\sigma)p(\sigma,\sigma-\eta)v(\eta)d\eta\right)d\sigma$$

for any $0 < t, a \le T$. Therefore, (57) is equal to (58), and the lemma is proven. \Box

Lemma 2. For the Doléans–Dade exponential $X(t) = \mathcal{E}{Y(t)} > 0$, we have

$$dX^{-1}(t) = -X^{-1}(t)dY(t) - d[X^{-1}, Y](t),$$
(59)

where $[U, V] = \frac{1}{4}([U + V] - [U - V])$ is the mutual variation of the semimartingales U and V.

Proof. Equality (59) can be derived from the stochastic integration by parts formula

$$d(UV) = U_{-}dV + V_{-}dU + d[U, V], \quad U_{-}(t) = U(t-),$$
(60)

(see e.g. [18, p. 185]), when applied to the identity $X^{-1}X = 1$:

$$0 = d(X^{-1}X) = X_{-}^{-1}dX + X_{-}dX^{-1} + d[X^{-1}, X]$$

= $X_{-}^{-1}X_{-}dY + X_{-}dX^{-1} + d[X^{-1}, \int X_{-}dY]$
= $X_{-}(dX_{-}^{-1} + X_{-}^{-1}dY + d[X^{-1}, Y]).$

Now, we can prove Theorem 1.

Proof. Due to the assumption on the jumps of v(t) and formula (9), the function $X(t) = \mathcal{E}{v(t)}$ is almost surely positive for all $t \ge 0$.

The claim is that u(t, a) satisfies (6) if and only if $\bar{u}(t, a) = u(t, a)X^{-1}(t)$ satisfies (53).

Let, therefore, $\bar{u}(t, a)$ obey (53). Remembering that X(0) = 1, we have to check that

$$\int_0^a X(t)\bar{u}(t,s)ds - \int_0^a \bar{u}(0,s)ds + \int_0^t X(\sigma)(\bar{u}(\sigma,a) - \bar{u}(\sigma,0))d\sigma = -\int_0^t \left(\int_0^a m(\sigma,s)X(\sigma)\bar{u}(\sigma,s)ds\right)d\sigma + \int_0^t \left(\int_0^a X(\sigma)\bar{u}(\sigma-s)ds\right)d\nu(\sigma).$$
(61)

The equality is trivial for t = 0. We prove therefore that the differentials of the left-hand side and the right-hand side coincide. To this end, we notice that

$$\int_0^a \bar{u}(t,s)ds = \int_0^a \bar{u}(0,s)ds - \int_0^t (\bar{u}(\sigma,a) - \bar{u}(\sigma,0))d\sigma - \int_0^t \left(\int_0^a m(\sigma,s)\bar{u}(\sigma,s)ds\right)d\sigma$$

has absolutely continuous trajectories and

$$d\left(\int_0^a \bar{u}(t,s)ds\right) = -(\bar{u}(t,a) - \bar{u}(t,0))dt - \left(\int_0^a m(t,s)\bar{u}(t,s)ds\right)dt.$$

Since dX(t) = X(t-)dv(t), $\bar{u}(t-, s) = \bar{u}(t, s)$ and [U, V] = 0 if one of the semimartingales U, V has absolutely continuous trajectories [18, p. 185], which simplifies the integration by parts formula (60), the following calculations justify (61):

$$d\left(\int_0^a X(t)\bar{u}(t,s)ds - \int_0^a \bar{u}(0,s)ds + \int_0^t X(\sigma)(\bar{u}(\sigma,a) - \bar{u}(\sigma,0))d\sigma\right)$$

= $\left(\int_0^a \bar{u}(t,s)dsX(t-)\right)d\nu(t) + X(t)\left(-(\bar{u}(t,a) - \bar{u}(t,0))dt - \left(\int_0^a m(t,s)\bar{u}(t,s)ds\right)dt\right)$
+ $X(t)(\bar{u}(t,a) - \bar{u}(t,0))dt = -\left(\int_0^a m(t,s)X(t)\bar{u}(t,s)ds\right)dt + \int_0^a X(t-)\bar{u}(t-,s)dsd\nu(t).$

The latter expression is equal to the differential of the right-hand side of (61).

Conversely, assume that u(t, s) satisfies (6). To check that in this case

$$\int_{0}^{a} (X^{-1}(t)u(t,s) - u(0,s))ds + \int_{0}^{t} X^{-1}(\sigma)(u(\sigma,a) - u(\sigma,0))d\sigma = -\int_{0}^{t} \left(\int_{0}^{a} m(\sigma,s)X^{-1}(\sigma)u(\sigma,s)ds \right) d\sigma,$$
(62)

let us again compare the differentials of the left-hand side and the right-hand side using formulae (59) and (60) as well as the equalities

$$d\left(\int_{0}^{a} u(t,s)ds\right) = -(u(t,a) - u(t,0))dt - \left(\int_{0}^{a} m(t,s)u(t,s)ds\right)dt + \int_{0}^{a} u(t-s)dsd\nu(t)$$

and

$$d[X^{-1}, \int_0^a u(\cdot, s)ds](t) = \int_0^a u(t-, s)ds[X^{-1}, \nu].$$

The latter equality reflects the fact that the absolute continuous part of $\int_0^a u(\cdot, s) ds$ can be removed from the quadratic variation [18, p. 185]. Thus, we obtain

$$\begin{aligned} d\left(\int_0^a X^{-1}(t)u(t,s)ds - \int_0^a u(0,s)ds + \int_0^t X^{-1}(\sigma)(u(\sigma,a) - u(\sigma,0))d\sigma\right) \\ &= X^{-1}(t)\left(-(u(t,a) - u(t,0))dt - \left(\int_0^a m(t,s)u(t,s)ds\right)dt + \int_0^a u(t-,s)dsd\nu(t)\right) \\ &+ \int_0^a u(t-,s)ds\,dX^{-1}(t) + d[X^{-1},\int_0^a u(\cdot,s)ds](t) + X^{-1}(t)(u(t,a) - u(t,0))dt \\ &= X^{-1}(t)\left(-\left(\int_0^a m(t,s)u(t,s)ds\right)dt + \int_0^a u(t-,s)dsd\nu(t)\right) \\ &+ \int_0^a u(t-,s)ds\left(-X^{-1}(t-)d\nu(t) - d[X^{-1},\nu]\right) + \int_0^a u(t-,s)ds\,d[X^{-1},\nu] = \\ &- \int_0^a m(t,s)X^{-1}(t)u(t,s)dsdt, \end{aligned}$$

so that (62) holds true.

Summarizing the above calculations, we now complete the proof of the theorem assuming that we are looking for a solution u(t, a) of (6) satisfying conditions (7), i.e.

$$\int_0^a (u(t,s) - \chi(s)) ds + \int_0^t (u(\sigma,a) - b(\sigma)) d\sigma = -\int_0^t \left(\int_0^a m(\sigma,s) u(\sigma,s) ds \right) d\sigma + \int_0^t \left(\int_0^a u(\sigma-s) ds \right) d\nu(\sigma).$$

Then from (62) we obtain that the locally Lebesgue integrable with probability 1 random function $\bar{u}(t, a) = X^{-1}(t)u(t, a)$ must obey

$$\int_0^a (\bar{u}(t,s)-\chi(s))ds + \int_0^t (\bar{u}(\sigma,a)-X^{-1}(\sigma)b(\sigma))d\sigma = -\int_0^t \left(\int_0^a m(\sigma,s)\bar{u}(\sigma,s)ds\right)d\sigma.$$

According to Lemma 1, the solution \bar{u} does exist and has representation (52), where $v_1(a) = \chi(a)$ and $v_2(t) = X^{-1}(t)b(t)$, so the solution of problem (6)–(7) exists as well and can be represented by formulae (10).

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