A Comparison of Probabilistic and Stochastic Formulations in Modeling Growth Uncertainty and Variability

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Abstract

We compare two approaches for inclusion of uncertainty/variability in modeling growth in size-structured population models. One entails imposing a probabilistic structure on growth rates in the population while the other involves formulating growth as a stochastic Markov diffusion process. We present a theoretical analysis that allows one to include comparable levels of uncertainty in the two distinct formulations in making comparisons of the two approaches.

1 Introduction

Classical size-structured population models (both linear and nonlinear versions) have been widely investigated in the past several decades as they have proved useful in modeling the

dynamics of a wide variety of populations such as cells, plants and marine species [15]. Among the best known of these is the basic linear version given by Sinko and Streifer [19] which we shall refer to as the Sinko-Streifer or SS model in this paper. The equation with boundary and initial conditions is given by

$$u_t(x,t) + (g(x,t)u(x,t))_x + m(x,t)u(x,t) = 0,$$

$$g(0,t)u(0,t) = \int_0^L \beta(x,t)u(x,t)dx, \tag{1.1}$$

$$u(x,0) = u_0(x),$$

where $u(x,t)$ denotes the population density of individuals with size x (for example, weight in grams in our motivating application here) at time t. The functions $m(x,t)$ and $\beta(x,t)$ represent the mortality rate and reproduction rate, respectively, of individuals with size x at time t. The parameter L is the maximum size that individuals may obtain in their lifetime, and the size of all the newborn individuals is assumed to be zero without loss of generality. The function $g(x,t)$ denotes the growth rate of individuals with size x at time t, so that each individual is assumed to grow according to the deterministic growth model

$$\frac{dx}{dt} = g(x,t). \tag{1.2}$$

Thus individuals with the same size at the same time have the same growth rate. This means that if there is no reproduction involved, then the variability of size at any time point is totally determined by the variability in the initial sizes. Thus, such models are incapable of manifesting any variability in growth rates that might occur in populations [4, 11]. This strongly suggests that the deterministic growth model (1.2) that is intrinsic to the Sinko-Streifer model is not sufficient to model the growth dynamics of many populations, and one needs in many cases to incorporate some type of variability or uncertainty into the growth process of individuals. For example, readily available experimental data (discussed below) for the early growth of shrimp exhibit a great deal of variability in size as time evolves even though the shrimp begin with approximately similar sizes. This phenomenon was also observed in studies [4, 8] of mosquitofish growth in rice fields, where the data exhibit both dispersion and bimodality in size as time increases. For these and other examples we are thus led to consider questions of variability or uncertainty in growth in size structured population models.

In this paper we consider two fundamentally different methods for this; one entails imposing a probabilistic structure on growth rates in the population while the other involves formulating growth as a stochastic Markov diffusion process. We do this in the context of an example for controlled shrimp growth, motivating the particular functional formulations that we use to illustrate ideas with available data from marine raceways that are used in typical studies of environmental influences on growth, death and fecundity of marine species.

1.1 Early Shrimp Growth Dynamics

Motivated in part by our earlier efforts [5] on modeling shrimp populations, in this section we use mean size data which depict the early growth of shrimp cultured at the Shrimp Mariculture Research Facility, Texas Agricultural Experiment Station in Corpus Christi, TX. The shrimp were grown in two different marine raceways with differing culture conditions, with all the shrimp at sampling time $t = 0$ in the postlarval (PL) stage (mean stocking size of shrimp for both raceways on April 20 was 0.000758 gm). Fifty shrimp were randomly sampled from each raceway and individually weighed at each time point in a longitudinal study. Of course, each sample of fifty contained possibly different shrimp and hence the data we use here is aggregate type longitudinal data (i.e., individuals are not tracked over time).

The average size (weight in grams) $\bar{x}_d^k$ of shrimp at time t_k is given by $\bar{x}_d^k = \dfrac{1}{50} \sum_{i=1}^{50} s_i^k$, where s_i^k is the size of shrimp i at time t_k. We used the exponential function

$$\bar{x}(t) = a \exp(bt) + c$$

to fit the data $\{(t_k, \bar{x}_d^k)\}$, where a, b, and c are unknown parameters that are to be estimated. Figure 1 depicts the exponential fit function $\bar{x}(t)$ (solid line) and data (*) for Raceway 1 and Raceway 2, respectively. The plots reveal that exponential functions appear to fit the data
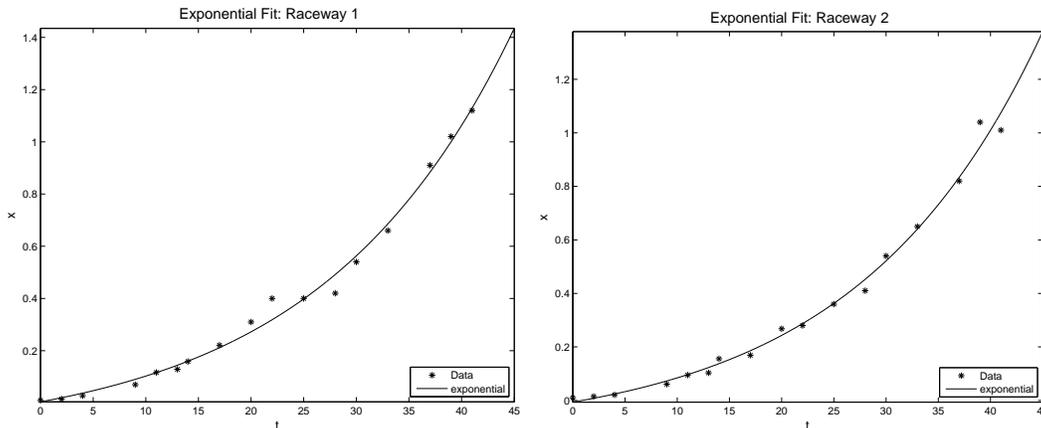

Figure 1: (left): Exponential fit of Raceway 1 data with $g(\bar{x}) = 0.054(\bar{x} + 0.133)$; (right): Exponential fit of Raceway 2 data with $g(\bar{x}) = 0.056(\bar{x} + 0.126)$.

in each of the raceways. Hence, the corresponding differential equation

$$\frac{d\bar{x}}{dt} = g(\bar{x}) = b_0(\bar{x} + c_0) \tag{1.3}$$

is one reasonable description of the early growth of shrimp. Here b_0 is a positive constant which denotes the intrinsic growth rate, and c_0 is a positive constant which we shall refer

to as the affine growth term. We remark that in our investigation of equivalent uncertainty formulations (probabilistic structure vs. stochastic formulation) in this paper, we employ these affine growth laws simply because they provide (in general non-unique) empirical fits to field data sets and are popular forms for use in shrimp dynamics models. The ideas presented are also tractable with other forms of empirical laws but these generalizations will not be pursued here.

Let $X(t)$ be a random variable which we use to denote the size of an individual in the population at time t. That is, each realization corresponds to the size at time t of an individual. Then we can write an analogue of (1.3) for mean growth dynamics as

$$\frac{d\mathcal{E}(X(t))}{dt} = b_0(\mathcal{E}(X(t)) + c_0). \tag{1.4}$$

The following arguments suggest that if we want to use the deterministic growth model (1.2) with the SS model to describe the early growth of shrimp, then we should choose the growth rate dynamics to be $\dfrac{dx}{dt} = g(x) = b_0(x + c_0)$. Then for each individual we have

$$x(t) = -c_0 + (x(0) + c_0)\exp(b_0 t). \tag{1.5}$$

Because we are considering the early growth of the shrimp population, we may ignore reproduction. Thus the size distribution at any time is totally determined by the initial size distribution. Let X_0 be a random variable which denotes the initial size distribution of individuals. Then by (1.5) we have

$$\mathcal{E}(X(t)) = -c_0 + (\mathcal{E}(X_0) + c_0)\exp(b_0 t),$$

which implies that

$$\frac{d\mathcal{E}(X(t))}{dt} = b_0(\mathcal{E}(X_0) + c_0)\exp(b_0 t) = b_0(\mathcal{E}(X(t)) + c_0).$$

Thus, with the growth rate function chosen as $g(x) = b_0(x + c_0)$ in the deterministic growth model, we obtain the same form as that in (1.4). In addition, by (1.5) we find that

$$\mathrm{Var}(X(t)) = \exp(2b_0 t)\mathrm{Var}(X_0), \tag{1.6}$$

which implies that the population does not disperse at all if the variance of the initial size distribution is zero (i.e., all shrimp are initially the same size). However, if $\mathrm{Var}(X_0)$ is nonzero, then propagating the initial distribution with the SS model and (1.5) should produce dispersion in a so-called *cryptodeterministic* formulation wherein random initial conditions are propagated deterministically [12].

To further investigate this approach, we inspect Figures 2 and 3 below which depict the observed size distributions of shrimp at different sampling time points for Raceway 1 and Raceway 2, respectively. These plots indicate that the shrimp population does exhibit a great deal of variability in size as time progresses even though they begin at a similar size (i.e.,
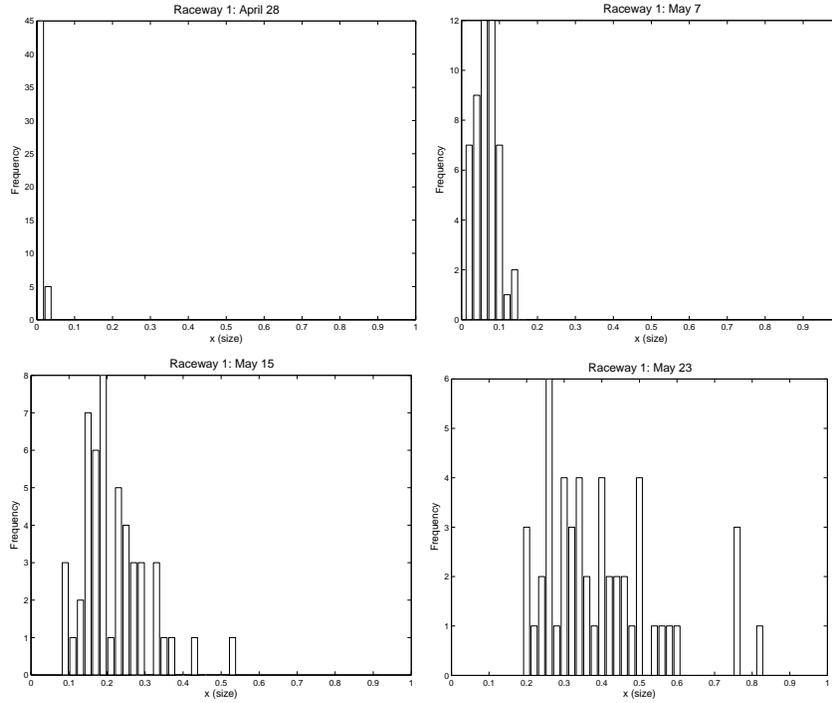
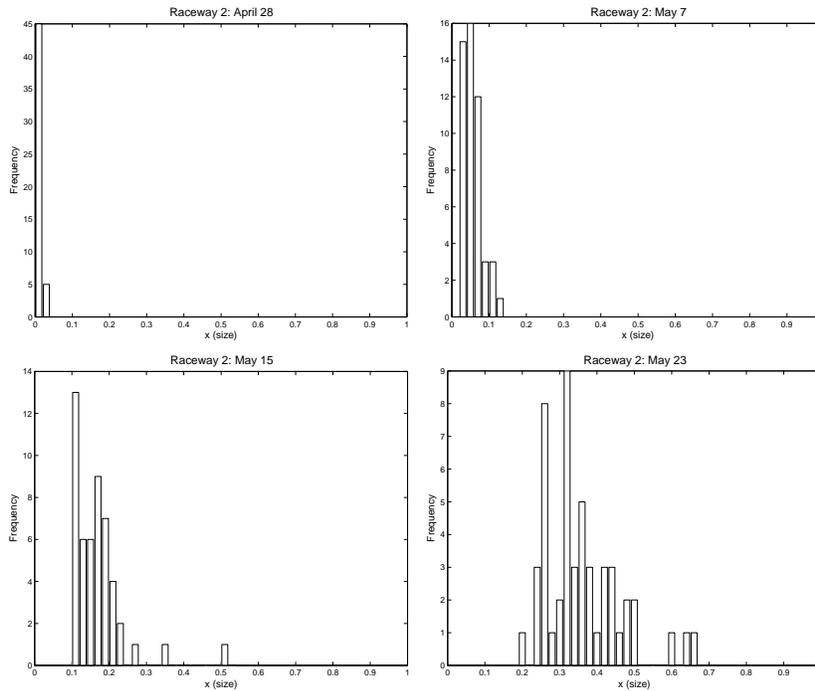Figure 2: Histograms for longitudinal data for Raceway 1.

Figure 3: Histograms for longitudinal data for Raceway 2.

$Var(X_0) \approx 0$). This then suggests that a cryptodeterministic formulation is not adequate and that we need to incorporate some variability into the growth of shrimp so that the

variability in size at any time is not only dependent on the variability in initial size but also on some variability in growth rates.

In this paper we consider two distinct approaches which have been proposed in the research literature [8, 9]. One entails imposing a probabilistic structure on growth rates in the population while the other involves formulating growth as a stochastic Markov diffusion process as a means to incorporate growth uncertainty/variability into size-structured population models. We use the early growth of shrimp as an *example* to illustrate the difference between these two different modeling formulations (we could equally well have used mosquitofish growth modeling as detailed in [4, 7, 8, 9]). Because we only consider the early growth of populations and are interested primarily in modeling growth uncertainty/variability, we will not consider reproduction and mortality rates in our formulations. Moreover, our interest here is in the relationship (equivalence) between what we term a probabilistic formulation and a corresponding stochastic formulation involving the Fokker-Planck equations. Thus we do not begin with infinitesimal dynamics generating the diffusion and drift coefficients in the Fokker-Planck equation and our approach is somewhat different from that in many modeling efforts, for example as in Chapter 5 of [1].

Our efforts here grew out of attempts at computational comparisons of the two approaches. For a reasonable comparison one should, of course, do this in a manner so that the level of uncertainty is equivalent in each method. Thus, one must investigate in what sense the "stochasticity" is present at comparable levels in each modeling approach.

The remainder of this paper is organized as follows. In Section 2 we introduce the two different approaches, which we shall refer to as a probabilistic formulation and a stochastic formulation, respectively, to model the growth uncertainty, and make a theoretical comparison of these two approaches. Finally we conclude the paper in Section 3 by some further observations and remarks.

2   Probabilistic vs. Stochastic Formulations

We describe two different formulations (e.g., [4, 6, 7, 8, 9, 17]) that have been considered in the literature to model uncertainty/variability in growth. One approach involves an assumption that each individual grows according to a deterministic growth model, but different individuals (even of the same size) may have different size dependent growth rates. Based on this, one partitions the entire population into (possibly a continuum of) subpopulations where individuals in each subpopulation have the same growth rate. We then assign a probability distribution to this partition of possible growth rates in the population. The growth process for individuals in a subpopulation with the rate g is described by the model

$$\frac{dx(t;g)}{dt} = g(x(t;g),t),\ g \in \mathcal{G}, \tag{2.1}$$

where $\mathcal{G}$ is the collection of admissible growth rates. Thus, the growth uncertainty is introduced into the population by the variability of growth rates among subpopulations of individuals. This corresponding phenomenon may be attributed to the effect of genetic differences or some chronic disease on the growth of individuals. For example, it was reported in [11] that non-lethal infection of *Penaeus vannamei* postlarvae by IHHNV may reduce growth and increase size variability in the population. With this assumption of a family of admissible growth rates and an associated probability distribution, one thus obtains a generalization of the Sinko-Streifer model, called the *Growth Rate Distribution (GRD) model*, which has been formulated and studied in [3, 4, 6, 7, 8]. The model consists of solving

$$v_t(x,t;g) + (g(x,t)v(x,t;g))_x = 0,$$
$$v(0,t;g) = 0, \tag{2.2}$$
$$v(x,0;g) = v_0(x;g),$$

for a given $g \in \mathcal{G}$ and then "summing" (with respect to the probability) the corresponding solutions over all $g \in \mathcal{G}$. Thus if $v(x,t;g)$ is the population density of individuals with size x at time t having growth rate g, the expectation of the total population density for size x at time t is given by

$$u(x,t) = \int_{g \in \mathcal{G}} v(x,t;g)d\mathcal{P}(g), \tag{2.3}$$

where $\mathcal{P}$ is the probability measure on $\mathcal{G}$. This probabilistic structure $\mathcal{P}$ on $\mathcal{G}$ is then the fundamental "parameter" to be determined from aggregate data for the population. Thus this *probabilistic formulation* involves a *stationary probabilistic structure* on a *family of deterministic dynamical systems*.

An alternative formulation, which we shall refer to as the *stochastic formulation*, is constructed based on the assumption that movement from one size class to another can be described by a stochastic diffusion process [1, 2, 9, 12, 17]. Let $X(t)$ be a Markov diffusion process which represents size at time t. Then $X(t)$ is described by the Ito stochastic differential equation (we refer to this equation as the stochastic growth model)

$$dX(t) = g(X(t),t)dt + \sigma(X(t),t)dW(t), \tag{2.4}$$

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where $W(t)$ is the standard Wiener process [1, 2, 12]. Here $g(x,t)$ denotes the average growth rate of individuals with size x at time t, and is given by

$$\lim_{\Delta t \to 0+} \frac{1}{\Delta t} \mathcal{E}(\Delta X(t)|X(t) = x) = g(x,t), \qquad (2.5)$$

where $\Delta X(t) = X(t + \Delta t) - X(t)$. The function $\sigma(x,t)$ represents the variability in the growth rate of individuals and is given by

$$\lim_{\Delta t \to 0+} \frac{1}{\Delta t} \mathcal{E}([\Delta X(t)]^2|X(t) = x) = \sigma^2(x,t). \qquad (2.6)$$

Hence, the growth process for each individual is stochastic, and each individual grows according to the stochastic growth model (2.4). In addition, individuals with the same size at the same time have the same variability in the growth. Thus, the growth uncertainty/variability is introduced into the population by the growth stochasticity of each individual. This phenomenon might be explained in some situations by the influence of fluctuations of the environment on the growth rate of individuals. For example, the growth rate of shrimp is affected by temperature, salinity, dissolved oxygen level, un-ionized ammonia level, etc., (e.g., see [13, 16, 18, 20]). With this assumption on the growth process, we obtain the Fokker-Planck (FP) or forward Kolmogorov model for the population density u, which was carefully derived in [17] among numerous other places and subsequently studied in many references (e.g., [1, 2, 9, 12]). The equation with appropriate boundary conditions is given by

$$
\begin{aligned}
&u_t(x,t) + (g(x,t)u(x,t))_x = \frac{1}{2}(\sigma^2(x,t)u(x,t))_{xx}, \\
&g(0,t)u(0,t) - \frac{1}{2}(\sigma^2(x,t)u(x,t))_x|_{x=0} = 0, \\
&g(L,t)u(L,t) - \frac{1}{2}(\sigma^2(x,t)u(x,t))_x|_{x=L} = 0, \\
&u(x,0) = u_0(x).
\end{aligned}
\qquad (2.7)
$$

In summary, from the above discussions, we readily see that in the probabilistic structure formulation resulting in the GRD model, the growth of each individual is a deterministic process, while in the stochastic formulation the growth of each individual is a stochastic process resulting in the FP model. Hence, these two formulations are conceptually quite different, and the choice of a formulation to describe the dynamics of a particular population should, if possible, be based on the mechanisms and/or scenarios that are the primary sources of the uncertainty/variability in growth.

Recall from Section 1.1 that the deterministic growth model used to describe the early growth of shrimp is

$$\frac{dx}{dt} = b_0(x + c_0), \qquad (2.8)$$

and the expectation and variance of the size distribution obtained from this deterministic growth model in a cryptodeterministic formulation (i.e., $x(0) = X_0$ is an initial random

variable that is propagated deterministically) are given by

$$\mathcal{E}(X(t)) = -c_0 + (\mathcal{E}(X_0) + c_0)\exp(b_0 t),$$
$$\mathrm{Var}(X(t)) = \mathrm{Var}(X_0)\exp(2b_0 t),$$

(2.9)

respectively. From our previous discussions, we recall that if we use the probabilistic formulation to model the growth uncertainty/variability, then we should put a distribution on the growth rates. Simple ways to do this are to put a distribution (with mean b_0) on the intrinsic growth rate or put a distribution (with mean c_0) on the affine growth term, or simultaneously put a distribution on both the intrinsic growth rate and the affine growth term. For simplicity here, we only consider a distribution on either the intrinsic growth rate or a distribution on the affine growth term. We will use B to denote a random variable for the intrinsic growth rate and use b to represent a realization of B in some range $\mathcal{R}_b$. Similarly, we will use C to represent a random variable for the affine growth and c to denote a realization of C in some range $\mathcal{R}_c$. We then consider two different probabilistic growth models:

$$\frac{dx(t;b)}{dt} = b(x(t;b) + c_0), \ b \in \mathcal{R}_b$$

(2.10)

and

$$\frac{dx(t;c)}{dt} = b_0(x(t;c) + c), \ c \in \mathcal{R}_c.$$

(2.11)

In Section 2.1 we shall discuss whether or not either of these probabilistic growth models can yield the same form of growth rate dynamics as that in (1.4). From (2.4) with $\sigma = 0$ and (2.8) we see that $g(x) = b_0(x + c_0)$ is a reasonable choice for the average growth rate in the stochastic growth model. In Section 2.2 we will find a proper form for σ in order to yield the same growth rate in the stochastic model as that in (1.4). The following relationship between a normal distribution and a lognormal distribution (p. 109, [10]) will be fundamental to our discussions in the next section. While this is sometimes taken as the *definition* of a lognormal distribution, one must in fact establish the relationship between the distribution of a normal (with mean μ and variance σ^2) and that of the exponentiation of a normal through transformation results (Theorem 2.1.5, p. 51, [10]). We summarize the results/definitions in the following statement.

Lemma 2.1 *If* $\ln Z \sim \mathcal{N}(\mu, \sigma^2)$, *then* Z *is by definition log-normally distributed, where its probability density function* $f_Z(z)$ *is defined by*

$$f_Z(z) = \frac{1}{z\sqrt{2\pi}\sigma}\exp\left(-\frac{(\ln z - \mu)^2}{2\sigma^2}\right),$$

and its mean and variance are given by

$$\mathcal{E}(Z) = \exp(\mu + \tfrac{1}{2}\sigma^2), \ \ Var(Z) = [\exp(\sigma^2) - 1]\exp(2\mu + \sigma^2).$$

We wish to compare the probabilistic and stochastic formulations described above. To do this it is important to compare them with the same level of uncertainty present in the models. One way to proceed is to compare the formulations with the same mean and variance in associated stochastic processes. The stochastic formulation defines directly a stochastic process for size satisfying a corresponding stochastic differential equation (2.4). In comparing the two formulations, it is thus useful to know whether the probabilistic formulation generates a corresponding stochastic process for size, and if it does, whether the process satisfies a stochastic or random differential equation, or even a mean growth dynamics equation such as (1.4). We carry out the analysis of the probabilistic formulation (2.1)-(2.3) by parameterizing the family $\mathcal{G}$ of admissible growth rates g using the form $g(x) = b(x + c)$ and considering distributions on either b or c.

2.1 Probabilistic Formulation and Associated Stochastic Processes

We first consider the probabilistic growth model (2.11) in Section 2.1.1 and show that this model can yield the same form of mean growth dynamics as that in (1.4), independent of the form of the distribution we put on the affine growth term. Then we consider the probabilistic growth model (2.10) in Section 2.1.2 and demonstrate that this model does *not* yield the same form of mean growth dynamics as that in (1.4) if a normal distribution is imposed on the intrinsic growth rate b. In Section 2.1.4 we consider a probabilistic formulation with $g(x,t) = (b - \sigma_0^2 t)(x + c_0)$ and argue that if we assume a normal distribution on the intrinsic growth rate b, then we do obtain the same form of mean growth dynamics as that in (1.4).

2.1.1 Distribution on the affine growth term c in $g(x) = b_0(x + c)$

In this section we consider the probabilistic growth model (2.11) with C having a probability density function $f_C(c)$ with mean and variance given by $\mathcal{E}(C) = c_0$ and $\mathrm{Var}(C) = \sigma_c^2$, respectively. Equation (2.11) implies that the size of each individual at time t in a subpopulation with affine growth term c is given by

$$x(t; c) = -c + (x(0; c) + c)\exp(b_0 t),$$

which can be rewritten as

$$x(t; c) = x(0; c)\exp(b_0 t) + c(\exp(b_0 t) - 1). \tag{2.12}$$

If the initial size of each individual is a fixed constant x_0, that is, $x(0; c) = x_0$ for any c in the chosen range, then the variability of size at any time t is totally determined by the variability in the affine growth term. That is, we obtain a stochastic random process for size which we denote by $X(t) = x(t; C)$. Hence, by (2.12) we have

$$X(t) = x_0 \exp(b_0 t) + C(\exp(b_0 t) - 1),$$

and moreover, $X(t)$ satisfies the random differential equation

$$\frac{dX(t)}{dt} = b_0(X(t) + C).\tag{2.13}$$

It follows that the probability density function $f_{X_t}(x)$ of $X(t)$ for any fixed t is given by

$$f_{X_t}(x) = \frac{1}{\exp(b_0 t) - 1} f_C\left(\frac{x - x_0 \exp(b_0 t)}{\exp(b_0 t) - 1}\right),\tag{2.14}$$

and the mean and variance of $X(t)$ are given by

$$\mathcal{E}(X(t)) = x_0 \exp(b_0 t) + c_0(\exp(b_0 t) - 1),$$
$$\mathrm{Var}(X(t)) = \sigma_c^2(\exp(b_0 t) - 1)^2.\tag{2.15}$$

Finally the mean $\mathcal{E}(X(t))$ satisfies the mean growth dynamics equation (1.4).

If the initial size distribution is the same for all the subpopulations and it is not a Dirac delta distribution, then the variability of size at any time t is determined by the variability in both the affine growth term and in the initial size distribution. That is, we have a stochastic process $X(t) = x(t; X_0, C)$ for size, where X_0 is a random variable with mean $\mathcal{E}(X_0) = x_0$, and by (2.12) we have

$$X(t) = X_0 \exp(b_0 t) + C(\exp(b_0 t) - 1).\tag{2.16}$$

Because X_0 generally has nothing to do with C, it is reasonable to assume that X_0 and C are two independent random variables. Then by (2.16) we find that

$$\mathcal{E}(X(t)) = \mathcal{E}(X_0) \exp(b_0 t) + c_0(\exp(b_0 t) - 1),$$
$$\mathrm{Var}(X(t)) = \mathrm{Var}(X_0) \exp(2b_0 t) + \sigma_c^2(\exp(b_0 t) - 1)^2.\tag{2.17}$$

Again $X(t)$ satisfies the random differential equation (2.13) as well as the corresponding mean growth dynamics equation (1.4). Thus, in either of these two cases we have the mean growth dynamics

$$\frac{d\mathcal{E}(X(t))}{dt} = b_0(\mathcal{E}(X(t)) + c_0)$$

as in (1.4) holding. Therefore, the probabilistic formulation based on (2.11) with any appropriate distribution on the affine growth term appears to be reasonable for the early growth of shrimp in the sense that it can yield the same form of mean growth dynamics as that in (1.4) which we have seen can be fit to data using (1.3). Note that the corresponding deterministic growth model of this probabilistic growth model is $\dot{x} = b_0(x + c_0)$. Moreover, by (2.9) and (2.17) we see that the expectation of the size distribution obtained from this model agrees with that obtained from its corresponding cryptodeterministic growth model. However, the variance of the size distribution obtained from this probabilistic growth model, which is determined not only by the variability in initial size distribution but also by the variability in the affine growth term, is greater than that obtained from its corresponding cryptodeterministic growth model which is determined only by the variability in the initial size distribution.

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2.1.2 Distribution on the intrinsic growth rate b in $g(x) = b(x + c_0)$

In this section we consider the probabilistic growth model (2.10) with $B \sim \mathcal{N}(b_0, \sigma_0^2)$ and $\mathcal{R}_b = \mathbb{R}$, deferring to subsequent discussion below the consequence of allowing negative values of b. Equation (2.10) implies that the size of each individual in a subpopulation with intrinsic growth rate b at time t is given by

$$x(t; b) = -c_0 + (x(0; b) + c_0) \exp(bt). \tag{2.18}$$

Note that $B \sim \mathcal{N}(b_0, \sigma_0^2)$ implies that for any fixed t

$$Bt \sim \mathcal{N}(b_0 t, \sigma_0^2 t^2). \tag{2.19}$$

Let $Y(t) = \exp(Bt)$. Thus, by (2.19) and Lemma 2.1 we know that $Y(t)$ is log-normally distributed for any fixed t, where its probability density function $f_{Y_t}(y)$ is given for $0 < y < \infty$ by

$$f_{Y_t}(y) = \frac{1}{y\sqrt{2\pi}\sigma_0 t} \exp\left(-\frac{[\ln y - b_0 t]^2}{2\sigma_0^2 t^2}\right), \tag{2.20}$$

with mean and variance given by

$$\mathcal{E}(Y(t)) = \exp\left(b_0 t + \frac{1}{2}\sigma_0^2 t^2\right), \tag{2.21}$$
$$\mathrm{Var}(Y(t)) = [\exp(\sigma_0^2 t^2) - 1] \exp(2b_0 t + \sigma_0^2 t^2).$$

If the initial size of each individual is a fixed constant x_0, that is, $x(0; b) = x_0$ for any b, then the variability of size at any time t is determined solely by the variability in the intrinsic growth rate. Thus the stochastic process for size is given by $X(t) = x(t; B)$ and by (2.18) we have

$$X(t) = -c_0 + (x_0 + c_0)Y(t).$$

Moreover from (2.20) we find that the probability density function $f_{X_t}(x)$ of $X(t)$ for any fixed t is given by

$$f_{X_t}(x) = \frac{1}{(x + c_0)\sqrt{2\pi}\sigma_0 t} \exp\left(-\frac{\left[\ln\left(\frac{x+c_0}{x_0+c_0}\right) - b_0 t\right]^2}{2\sigma_0^2 t^2}\right), \tag{2.22}$$

with mean and variance given by

$$\mathcal{E}(X(t)) = -c_0 + (x_0 + c_0) \exp\left(b_0 t + \frac{1}{2}\sigma_0^2 t^2\right) \tag{2.23}$$
$$\mathrm{Var}(X(t)) = (x_0 + c_0)^2 [\exp(\sigma_0^2 t^2) - 1] \exp(2b_0 t + \sigma_0^2 t^2).$$

Again we find that $X(t)$ satisfies a random differential equation

$$\frac{dX(t)}{dt} = B(X(t) + c_0). \tag{2.24}$$

However, in this case it is *not* true that $\mathcal{E}(X(t))$ generally satisfies the usual mean growth dynamics (1.4). As we shall see below, $\mathcal{E}(X(t))$ does satisfy a related differential equation. But first we consider the case when the initial size distribution is the same for all the subpopulations and is not a Dirac delta distribution, so that the variability in size at any time t is determined by the variability in both the intrinsic growth rate and the initial size distribution. The size stochastic process is defined by $X(t) = x(t; X_0, B)$ and hence, by (2.18) we have

$$X(t) = -c_0 + (X_0 + c_0)Y(t), \tag{2.25}$$

where X_0 is a random variable which denotes the initial size. Again it is reasonable to assume that X_0 and $Y(t)$ are independent random variables. Then by (2.25) and (2.21) we find that

$$
\begin{aligned}
\mathcal{E}(X(t)) &= -c_0 + (\mathcal{E}(X_0) + c_0) \exp\left(b_0 t + \frac{1}{2}\sigma_0^2 t^2\right), \\
\mathrm{Var}(X(t)) &= (\mathcal{E}(X_0) + c_0)^2 [\exp(\sigma_0^2 t^2) - 1] \exp(2b_0 t + \sigma_0^2 t^2) \\
&\quad + \mathrm{Var}(X_0)[\exp(\sigma_0^2 t^2) - 1] \exp(2b_0 t + \sigma_0^2 t^2) \\
&\quad + \exp\left(2b_0 t + \sigma_0^2 t^2\right) \mathrm{Var}(X_0).
\end{aligned}
\tag{2.26}
$$

It follows from (2.23) and (2.26) that

$$\frac{d\mathcal{E}(X(t))}{dt} = (b_0 + \sigma_0^2 t)(\mathcal{E}(X(t)) + c_0). \tag{2.27}$$

Thus, by using the probabilistic growth model (2.10) with normal distribution $\mathcal{N}(b_0, \sigma_0^2)$ for B, we cannot obtain the same form of mean growth rate as that we obtained in (1.4). We note that computing the mean and variance of $X(t)$ in these examples depends directly on the ability to compute similar quantities for $Y(t) = \exp(Bt)$ and is facilitated by the special form of the distribution of B (see [10] for discussions of properties of functions of random variables). Moreover, we remind the reader that we are interested in a formulation where the probabilistic formulation is equivalent to a stochastic formulation. We chose (1.4) as an example to illustrate our approach because it yields a reasonable fit to data. A similar investigation could be pursued using other individual dynamics in place of (1.4).

From (2.23) and (2.26), we see that both the expectation and the variance in size distribution obtained from the probabilistic growth model (2.10) with $B \sim \mathcal{N}(b_0, \sigma_0^2)$ is dependent on the variability in the intrinsic growth rate in the first case (2.23), and in the second case (2.26) they depend not only on the variability in the intrinsic growth rate but also on the variability in the initial size distribution. Note that the corresponding cryptodeterministic formulation of this probabilistic growth model is given by $\dot{x} = b_0(x + c_0)$, $x(0) = X_0$. Hence, (2.9), (2.23) and (2.26) reveal that the expectation in size distribution of these probabilistic formulations is always greater than that obtained from its corresponding cryptodeterministic formulation, and the same thing is true for the variance.

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2.1.3 Distribution on b, c, and x_0 simultaneously in $g(x) = b(x + c)$

We have considered in the previous sections special cases for random differential equation analogues of the deterministic system

$$\frac{dx(t)}{dt} = b(x + c), \quad x(0) = x_0. \tag{2.28}$$

More generally, using the solution

$$x(t; b, c, x_0) = (x_0 + c)\exp(bt) - c, \tag{2.29}$$

of (2.28) and assuming that B, C and X_0 are random variables for b, c and x_0, respectively, we can always define a stochastic process

$$X(t; B, C, X_0) = (X_0 + C)\exp(Bt) - C, \tag{2.30}$$

and argue that it satisfies the random differential equation

$$\frac{dX(t)}{dt} = B(X(t) + C), \quad X(0) = X_0. \tag{2.31}$$

But in general one cannot say anything about $\mathcal{E}(X(t))$ and $\mathrm{Var}(X(t))$ without special assumptions on B, C and X_0 that would enable one to ascertain statistical properties of $X(t)$ and statistical relationships between $X(t), B, X_0$ and C.

2.1.4 Distribution on the intrinsic growth rate b in $g(x, t) = (b - \sigma_0^2 t)(x + c_0)$

From (2.27), it appears that if we set the probabilistic growth model to be

$$\frac{dx(t; b)}{dt} = (b - \sigma_0^2 t)(x + c_0), \ b \in \mathbb{R}, \tag{2.32}$$

with $B \sim \mathcal{N}(b_0, \sigma_0^2)$, then we may obtain the same form of mean growth dynamics as we obtained in (1.4). We proceed to argue that this is indeed the case. Equation (2.32) implies that the size of each individual in a subpopulation with intrinsic growth rate b at time t is given by

$$x(t; b) = -c_0 + (x(0; b) + c_0)\exp(bt - \tfrac{1}{2}\sigma_0^2 t^2). \tag{2.33}$$

Note that $B \sim \mathcal{N}(b_0, \sigma_0^2)$ implies that for any fixed t

$$Bt - \tfrac{1}{2}\sigma_0^2 t^2 \sim \mathcal{N}(b_0 t - \tfrac{1}{2}\sigma_0^2 t^2, \sigma_0^2 t^2). \tag{2.34}$$

Let $Y(t) = \exp(Bt - \tfrac{1}{2}\sigma_0^2 t^2)$. Thus, by (2.34) and Lemma 2.1 we know that $Y(t)$ is log-normally distributed for any fixed t, where its probability density function $f_{Y_t}(y)$ is given by

$$f_{Y_t}(y) = \frac{1}{y\sqrt{2\pi}\sigma_0 t}\exp\left(-\frac{[\ln y - (b_0 t - \tfrac{1}{2}\sigma_0^2 t^2)]^2}{2\sigma_0^2 t^2}\right), \tag{2.35}$$

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with mean and variance given by

$$\mathcal{E}\left(Y(t)\right) = \exp\left(b_0 t\right),$$

$$\mathrm{Var}\left(Y(t)\right) = [\exp(\sigma_0^2 t^2) - 1]\exp(2b_0 t). \tag{2.36}$$

If the initial size of each individual is a fixed constant x_0, that is, $x(0; b) = x_0$ for any b, then the variability in size at any time t is totally determined by the variability in the intrinsic growth rate, so that the size stochastic process is $X(t) = x(t; B)$. From (2.33) we have

$$X(t) = -c_0 + (x_0 + c_0)Y(t),$$

and from (2.35) we find that the probability density function $f_{X_t}(x)$ of $X(t)$ for any fixed t is given by

$$f_{X_t}(x) = \frac{1}{(x + c_0)\sqrt{2\pi}\sigma_0 t} \exp\left(-\frac{\left[\ln\left(\frac{x+c_0}{x_0+c_0}\right) - (b_0 t - \frac{1}{2}\sigma_0^2 t^2)\right]^2}{2\sigma_0^2 t^2}\right), \tag{2.37}$$

with mean and variance given by

$$\mathcal{E}(X(t)) = -c_0 + (x_0 + c_0)\exp\left(b_0 t\right),$$

$$\mathrm{Var}(X(t)) = (x_0 + c_0)^2[\exp(\sigma_0^2 t^2) - 1]\exp(2b_0 t). \tag{2.38}$$

Assuming that the initial size distribution is the same for all the subpopulations and it is not a Dirac delta distribution, then the variability in size at any time t is determined by the variability in both the intrinsic growth rate and the initial size distribution. The corresponding size stochastic process is given by $X(t) = x(t; X_0, B)$ where X_0 is a random variable which denotes the initial size. From (2.33) we have

$$X(t) = -c_0 + (X_0 + c_0)Y(t). \tag{2.39}$$

It is reasonable to assume that X_0 and $Y(t)$ are two independent random variables. Then by (2.36) and (2.39) we find that

$$\mathcal{E}(X(t)) = -c_0 + (\mathcal{E}(X_0) + c_0)\exp\left(b_0 t\right),$$

$$\mathrm{Var}(X(t)) = (\mathcal{E}(X_0) + c_0)^2[\exp(\sigma_0^2 t^2) - 1]\exp(2b_0 t) \tag{2.40}$$

$$+\mathrm{Var}(X_0)[\exp(\sigma_0^2 t^2) - 1]\exp(2b_0 t) + \exp(2b_0 t)\mathrm{Var}(X_0).$$

Moreover, we find the mean growth dynamics

$$\frac{d\mathcal{E}(X(t))}{dt} = b_0(\mathcal{E}(X(t)) + c_0).$$

Thus, by using probabilistic growth model (2.32) with normal distribution $\mathcal{N}(b_0, \sigma_0^2)$ on B, we can obtain the same form of mean growth dynamics as obtained in (1.4).

Note that the corresponding cryptodeterministic formulation of this probabilistic growth model is given by $\dot{x} = (b_0 - \sigma_0^2 t)(x + c_0)$, $x(0) = X_0$. Hence, the expectation and variance of the size stochastic process $X(t)$ obtained from this cryptodeterministic model at time t are

$$\mathcal{E}(X(t)) = -c_0 + (\mathcal{E}(X_0) + c_0) \exp\left(b_0 t - \frac{1}{2}\sigma_0^2 t^2\right),$$

$$\mathrm{Var}(X(t)) = \mathrm{Var}(X_0) \exp\left(2b_0 t - \sigma_0^2 t^2\right). \tag{2.41}$$

Thus, (2.41) and (2.40) demonstrate that the expectation in these size stochastic processes obtained from this probabilistic growth model formulation is greater than that obtained from its corresponding cryptodeterministic growth model, and the same thing is true for the variance.

Based on the discussions in Sections 2.1.2 and 2.1.4, we know that if $B \sim \mathcal{N}(b_0, \sigma_0^2)$, then the probabilistic growth model (2.32) is more reasonable to use in comparisons for the shrimp growth than the probabilistic growth model (2.10) in the sense that (2.32) can yield the same form of mean growth dynamics as shown in (1.4) but (2.10) cannot.

2.2   Stochastic Formulation: Stochastic Growth Process

Finally we turn to an analysis of the stochastic formulation with the size stochastic process defined directly by a classical stochastic differential equation (SDE). We will argue that if we set $g(x) = b_0(x + c_0)$ with an appropriately chosen form for σ, then we can obtain the same form of mean growth dynamics as we obtained in (1.4). We will consider two different choices for σ that can each be combined with the chosen form for g to obtain the same form of mean growth dynamics as in (1.4). For the first case, we choose $\sigma(x) = \bar{\sigma}_0(x + c_0)$, where $\bar{\sigma}_0$ is a positive constant. With this form of σ, the mean of the size process obtained from this stochastic growth model is the same as that obtained from probabilistic growth model (2.32) in Section 2.1.4, but this is not true for the variance of the size process. Specifically, the variance of the size process obtained from probabilistic growth model (2.32) at time t is dependent on t^2 as shown in (2.38) and (2.40), but as is established in (2.47) and (2.49) below, the variance of the size process obtained from this stochastic growth model at time t is dependent on t. For the second case, we choose $\sigma(x, t) = \sqrt{2t}\bar{\sigma}_0(x + c_0)$. With this form of σ we obtain the same mean and variance for the size process as that obtained from probabilistic growth model (2.32) with $\sigma_0 = \bar{\sigma}_0$. We remark that this choice of σ is not based on any particular biological mechanism; rather, if one begins with the probabilistic structure with affine growth (1.4), to obtain an equivalent stochastic formulation one simply chooses this σ.

2.2.1 The SDE with $\sigma(x) = \bar{\sigma}_0(x + c_0)$

In this section, the function $\sigma(x)$ is chosen as $\sigma(x) = \bar{\sigma}_0(x + c_0)$. Let $h(x, t) = \ln(x + c_0)$. Then we have

$$\frac{\partial h(x,t)}{\partial t} = 0, \quad \frac{\partial h(x,t)}{\partial x} = \frac{1}{x + c_0}, \quad \frac{\partial^2 h(x,t)}{\partial x^2} = -\frac{1}{(x + c_0)^2}.$$

By Ito's Formula (Theorem 8.3 in [2]) we find that

$$dh(X(t), t) = (b_0 - \tfrac{1}{2}\bar{\sigma}_0^2)dt + \bar{\sigma}_0 dW(t).$$

Integrating both sides of the above equation we find

$$\ln\left(\frac{X(t) + c_0}{X(0) + c_0}\right) = (b_0 - \tfrac{1}{2}\bar{\sigma}_0^2)t + \bar{\sigma}_0 W(t),$$

which implies that

$$\frac{X(t) + c_0}{X(0) + c_0} = \exp((b_0 - \tfrac{1}{2}\bar{\sigma}_0^2)t + \bar{\sigma}_0 W(t)). \tag{2.42}$$

Note that $W(t) \sim \mathcal{N}(0, t)$. Hence, we have that

$$(b_0 - \tfrac{1}{2}\bar{\sigma}_0^2)t + \bar{\sigma}_0 W(t) \sim \mathcal{N}\left((b_0 - \tfrac{1}{2}\bar{\sigma}_0^2)t, \bar{\sigma}_0^2 t\right). \tag{2.43}$$

Let $Y(t) = \exp((b_0 - \tfrac{1}{2}\bar{\sigma}_0^2)t + \bar{\sigma}_0 W(t))$. Then by (2.43) and Lemma 2.1, we have that $Y(t)$ is log-normally distributed for any fixed t, with its probability density function $f_{Y_t}(y)$ defined by

$$f_{Y_t}(y) = \frac{1}{y\sqrt{2\pi}(\bar{\sigma}_0\sqrt{t})} \exp\left(-\frac{[\ln y - (b_0 - \tfrac{1}{2}\bar{\sigma}_0^2)t]^2}{2\bar{\sigma}_0^2 t}\right), \tag{2.44}$$

and with its mean and variance given by

$$\mathcal{E}(Y(t)) = \exp(b_0 t),$$
$$\mathrm{Var}(Y(t)) = [\exp(\bar{\sigma}_0^2 t) - 1]\exp(2b_0 t). \tag{2.45}$$

Next, we consider two cases for $X(0)$. One case is that $X(0)$ is a fixed constant x_0, and the other is that $X(0)$ is a random variable X_0. If $X(0) = x_0$, then by (2.42) and (2.44) we find that the probability density function $f_{X_t}(x)$ of $X(t)$ for any fixed t is given by

$$f_{X_t}(x) = \frac{1}{(x + c_0)\sqrt{2\pi}(\bar{\sigma}_0\sqrt{t})} \exp\left(-\frac{\left[\ln\left(\frac{x+c_0}{x_0+c_0}\right) - (b_0 - \tfrac{1}{2}\bar{\sigma}_0^2)t\right]^2}{2\bar{\sigma}_0^2 t}\right). \tag{2.46}$$

By (2.45) we find that the mean and variance of $X(t)$ for any fixed t are given by

$$\mathcal{E}(X(t)) = -c_0 + (x_0 + c_0)\exp(b_0 t),$$
$$\mathrm{Var}(X(t)) = (x_0 + c_0)^2[\exp(\bar{\sigma}_0^2 t) - 1]\exp(2b_0 t). \tag{2.47}$$

If $X(0) = X_0$ is a random variable, then by (2.42) we have

$$X(t) = -c_0 + (X_0 + c_0)Y(t). \tag{2.48}$$

As in the previous discussions, it is reasonable to assume that X_0 and $Y(t)$ are independent random variables. Then by (2.48) and (2.45) we find that

$$\mathcal{E}(X(t)) = -c_0 + (\mathcal{E}(X_0) + c_0)\exp(b_0 t),$$

$$\mathrm{Var}(X(t)) = (\mathcal{E}(X_0) + c_0)^2[\exp(\bar{\sigma}_0^2 t) - 1]\exp(2b_0 t) \tag{2.49}$$

$$+\mathrm{Var}(X_0)[\exp(\bar{\sigma}_0^2 t) - 1]\exp(2b_0 t) + \mathrm{Var}(X_0)\exp(2b_0 t).$$

Note that (2.47) and (2.49) each yield the mean growth dynamics

$$\frac{d\mathcal{E}(X(t))}{dt} = b_0(\mathcal{E}(X(t)) + c_0). \tag{2.50}$$

Thus we obtain the same form of mean growth dynamics as obtained in (1.4). In addition, we see that the corresponding cryptodeterministic growth model to this stochastic process is $\dot{x} = b_0(x + c_0), x(0) = X_0$. Hence, by (2.9) and (2.49) we find that the expectation in the size process obtained from this stochastic growth model agrees with that obtained from its corresponding cryptodeterministic formulation. However, the variance obtained from this stochastic formulation, which is determined by variability in initial size and uncertainty in growth of each individual, is greater than that obtained from its corresponding cryptodeterministic formulation which is determined only by the variability in initial size.

2.2.2 The SDE with $\sigma(x, t) = \sqrt{2t}\bar{\sigma}_0(x + c_0)$

Based on the discussions in the above section, we see that the variance in the size process at time t obtained from the stochastic formulation with $\sigma(x) = \bar{\sigma}_0(x + c_0)$ being dependent on t results from $\mathrm{Var}(W(t)) = t$ and the fact that σ does not depend on t at all. Therefore, in order to have the variance of the size process at time t dependent on t^2 as that in probabilistic growth model (2.32), it appears that we need to choose $\sigma(x, t) = \sqrt{2t}\bar{\sigma}_0(x + c_0)$. We shall argue that this is in fact the case. Again let $h(x, t) = \ln(x + c_0)$. Then by Ito's Formula we find that

$$dh(X(t), t) = (b_0 - \bar{\sigma}_0^2 t)dt + \sqrt{2t}\bar{\sigma}_0 dW(t).$$

Integrating both sides of the above equation we obtain

$$\ln\left(\frac{X(t) + c_0}{X(0) + c_0}\right) = (b_0 t - \tfrac{1}{2}\bar{\sigma}_0^2 t^2) + \bar{\sigma}_0\int_0^t \sqrt{2s}dW(s),$$

which implies that

$$\frac{X(t) + c_0}{X(0) + c_0} = \exp\left((b_0 t - \tfrac{1}{2}\bar{\sigma}_0^2 t^2) + \bar{\sigma}_0\int_0^t \sqrt{2s}dW(s)\right). \tag{2.51}$$

By Theorem 4.5 in [14], for any fixed t we find that

$$\bar{\sigma}_0 \int_0^t \sqrt{2s}dW(s) \sim \mathcal{N}(0, \bar{\sigma}_0^2 t^2),$$

which implies that

$$(b_0 t - \tfrac{1}{2}\bar{\sigma}_0^2 t^2) + \bar{\sigma}_0 \int_0^t \sqrt{2s}dW(s) \sim \mathcal{N}\left(b_0 t - \tfrac{1}{2}\bar{\sigma}_0^2 t^2, \bar{\sigma}_0^2 t^2\right). \tag{2.52}$$

Let $Y(t) = \exp\left((b_0 t - \tfrac{1}{2}\bar{\sigma}_0^2 t^2) + \bar{\sigma}_0 \int_0^t \sqrt{2s}dW(s)\right)$. Then by (2.52) and Lemma 2.1, we find that $Y(t)$ is log-normally distributed for any fixed t, where its probability density function $f_{Y_t}(y)$ is defined by

$$f_{Y_t}(y) = \frac{1}{y\sqrt{2\pi}\bar{\sigma}_0 t} \exp\left(-\frac{[\ln y - (b_0 t - \tfrac{1}{2}\bar{\sigma}_0^2 t^2)]^2}{2\bar{\sigma}_0^2 t^2}\right), \tag{2.53}$$

with mean and variance given by

$$\mathcal{E}(Y(t)) = \exp(b_0 t),$$
$$\mathrm{Var}(Y(t)) = [\exp(\bar{\sigma}_0^2 t^2) - 1]\exp(2b_0 t). \tag{2.54}$$

As before we consider two cases for $X(0)$: $X(0) = x_0$ is a fixed constant, and $X(0) = X_0$ is a random variable. If $X(0) = x_0$, then by (2.51) and (2.53) we find that the probability density function $f_{X_t}(x)$ of $X(t)$ for any fixed t is given by

$$f_{X_t}(x) = \frac{1}{(x+c_0)\sqrt{2\pi}\bar{\sigma}_0 t} \exp\left(-\frac{\left[\ln\left(\frac{x+c_0}{x_0+c_0}\right) - (b_0 t - \tfrac{1}{2}\bar{\sigma}_0^2 t^2)\right]^2}{2\bar{\sigma}_0^2 t^2}\right). \tag{2.55}$$

From (2.51) and (2.54) we find that the mean and variance of $X(t)$ for any fixed t are given by

$$\mathcal{E}(X(t)) = -c_0 + (x_0 + c_0)\exp(b_0 t),$$
$$\mathrm{Var}(X(t)) = (x_0 + c_0)^2[\exp(\bar{\sigma}_0^2 t^2) - 1]\exp(2b_0 t). \tag{2.56}$$

If $X(0) = X_0$ is a random variable, then by (2.51) we have

$$X(t) = -c_0 + (X_0 + c_0)Y(t), \tag{2.57}$$

where again we assume that X_0 and $Y(t)$ are independent random variables. Then by (2.57) and (2.54) we find that

$$\mathcal{E}(X(t)) = -c_0 + (\mathcal{E}(X_0) + c_0)\exp(b_0 t),$$
$$\mathrm{Var}(X(t)) = (\mathcal{E}(X_0) + c_0)^2[\exp(\bar{\sigma}_0^2 t^2) - 1]\exp(2b_0 t) \tag{2.58}$$
$$+ \mathrm{Var}(X_0)[\exp(\bar{\sigma}_0^2 t^2) - 1]\exp(2b_0 t) + \mathrm{Var}(X_0)\exp(2b_0 t).$$

Hence, each of (2.56) and (2.58) result in

$$\frac{d\mathcal{E}(X(t))}{dt} = b_0(\mathcal{E}(X(t)) + c_0). \tag{2.59}$$

Thus, with this choice of σ in the SDE of the stochastic formulation we obtain the same form of mean growth dynamics as obtained in (1.4). Observe that the corresponding deterministic growth model in this stochastic growth formulation is $\dot{x} = b_0(x + c_0)$. Hence, by (2.9) and (2.58) we find that that the expectation of the size process obtained from this stochastic formulation agrees with that obtained from its corresponding cryptodeterministic model. However, the variance obtained from this stochastic formulation, which is determined by both variability in initial size and uncertainty in growth of each individual, is greater than that obtained from its corresponding cryptodeterministic growth formulation. In addition, we see that with this form of σ we obtain the same size process as we obtained from probabilistic growth model (2.32) if $\bar{\sigma}_0 = \sigma_0$ and their initial size distributions are the same.

2.3 Summary Remarks

The arguments and discussions in Sections 2.1 and 2.2 reveal that the expectation of the size stochastic process obtained from both the stochastic formulation and the probabilistic growth model with a distribution on the affine growth term agree with that obtained from their corresponding cryptodeterministic growth models, but this is not true for the probabilistic growth model with a distribution on the intrinsic growth rate. Based on discussions from Sections 2.1.4 and 2.2.2, we also see that the size distribution obtained from the stochastic formulation is exactly the same as that obtained from probabilistic formulation if we consider the models:

Stochastic formulation: $dX(t) = b_0(X(t) + c_0)dt + \sqrt{2t}\sigma_0(X(t) + c_0)dW(t)$

Probabilistic formulation: $\frac{dx(t; b)}{dt} = (b - \sigma_0^2 t)(x(t; b) + c_0), b \in \mathbb{R}$ with $B \sim \mathcal{N}(b_0, \sigma_0^2)$,

with their initial size distributions $X(0)$ the same (either deterministic or random).

We should observe that if in the probabilistic formulation we impose a normal distribution $\mathcal{N}(b_0, \sigma_0^2)$ for the intrinsic growth rate B, this is not completely reasonable in our motivating application because the intrinsic growth rate can then be negative which results in the size having positive probability of being negative as shown in (2.22) and (2.37) which actually hold for $-c_0 < x < \infty$. However, if σ_0 is chosen to be much smaller than b_0, then the probability of the intrinsic growth rate being negative is negligible. For example, even if we set σ_0 to be 30% of the mean b_0, then at least 99% of samples from $\mathcal{N}(b_0, \sigma_0^2)$ are expected to be positive. Thus, there is a slight inaccuracy between the model size process obtained with a normal distribution on the intrinsic growth rate and the size process in the motivating application (i.e., in which b is generally nonnegative). This is also true for the size stochastic process obtained from stochastic formulation involving a Wiener process which also leads to the size having the positive probability of being negative as evidenced in (2.46) and (2.55).

In actuality using these formulations for any computational population studies, one would usually modify the normal distributions to prevent positive probabilities for negative sizes. In our theoretical studies here we do not consider this detail because this would make any theoretical comparisons between the probabilistic formulations and stochastic formulations in a reasonable way an extremely formidable task (recall that all of our analysis depends heavily on Lemma 2.1 which is very specific to the normal distribution). As noted above, if we set σ_0 in the probabilistic formulation and $\bar{\sigma}_0$ in the stochastic formulation to be much smaller than b_0, then all of the analyses in Sections 2.1 and 2.2 are a reasonable approximation over relatively short time periods to models with essentially positive intrinsic growth rates and positive sizes. These models in turn are a reasonable approximation to the processes in the motivating application involving size-structured populations. More importantly, the analyses here provide a reasonable foundation for choosing means and variances in the two formulations to assure comparable uncertainty is being included when making computational comparisons of the two very distinct approaches.

3 Concluding Remarks

In this note we considered two distinct approaches, a probabilistic formulation and a stochastic formulation, to incorporate growth uncertainty into size-structured population models. The differences between these two approaches are summarized as follows:

- The growth uncertainty in the probabilistic formulation is introduced into the population dynamics by a variability of growth rates among individuals in the population and this results in a growth rate distribution on a family of admissible rates. For the stochastic formulation, uncertainty is introduced into the population by the stochasticity of the growth process for each individual and this results in the Fokker-Planck model for the size densities.

- The growth process for each individual in the probabilistic formulation is a deterministic one which actually leads to a stochastic process for size, while the growth process for each individual in the stochastic formulation is directly formulated as a size stochastic process.

- The expectation of the size process obtained from both the stochastic formulation and the probabilistic growth model with a distribution on the affine growth term agree with that obtained from their corresponding cryptodeterministic growth models, but this is not true for the probabilistic growth model with a distribution on the intrinsic growth rate. However, by proper choice of variability in each formulation, one can obtain size stochastic processes with comparable means and variances even in the case of a distribution on the intrinsic growth rates in the probabilistic formulations.

Future efforts include plans to incorporate uncertainty in the mortality and reproduction rates into these models and investigate the differences between the distinct approaches in

modeling these uncertainties. We are currently using the theoretical results from this study as a foundation for computational comparisons of the two formulations discussed here.

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