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Lévy processes and stochastic von Bertalanffy models of growth, with application to fish population analysis

Tommaso Russo [a,*], Paolo Baldi [b], Antonio Parisi [c], Giuseppe Magnifico [d], Stefano Mariani [e], Stefano Cataudella [a]

[a] Laboratorio di Ecologia Sperimentale e Acquacoltura, Dipartimento di Biologia, Università di Roma Tor Vergata, Italy
[b] Dipartimento di Matematica, Università di Roma Tor Vergata, Italy
[c] Dipartimento di Studi Economico-Finanziari e Metodi Quantitativi Facoltá di Economia, Università di Roma Tor Vergata, Italy
[d] Consiglio Nazionale delle Ricerche, CNR, Roma, Italy
[e] School of Biology and Environmental Science, University College of Dublin, Ireland

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ABSTRACT

The study of animal growth is a longstanding crucial topic of theoretical biology. In this paper we introduce a new class of stochastic growth models that enjoy two crucial properties: the growth path of an individual is monotonically increasing and the mean length at time t follows the classic von Bertalanffy model. Besides the theoretical development, the models are also tested against a large set of length-at-age data collected on Atlantic herring (*Clupea harengus*): the mean lengths and variances of the cohorts were directly estimated by least squares. The results show that the use of subordinators can lead to models enjoying interesting properties, in particular able to catch some specific features often observed in fish growth data. The use of subordinators seems to allow for an increased fidelity in the description of fish growth, whilst still conforming to the general parameters of the traditional von Bertalanffy equation.

1. Introduction

The modelling of growth and the analysis of intra-population pattern of size variability through time are the central topics in animal population biology, since the internal size structure of populations can have a decisive influence on the population dynamics (DeAngelis et al., 1993; Imsland et al., 1998; Uchmanski, 2000; Kendall and Fox, 2002; Fujiwara et al., 2004). In general, the von Bertalanffy growth function (VBGF, von Bertalanffy, 1957) is the best acknowledged and used relationship to describe the growth of fish and other animals. This equation states that the size of an individual increases in time according to the equation

$$x_t = L_\infty\left(1 - e^{-k(t+t_0)}\right), \tag{1.1}$$

where L_∞ is the extremal length that is attained as time goes to infinity, $-t_0$ is the time of conception, at which the size should be 0 and k is a parameter that gives the speed of the process: the larger the value of k, the quickest the growth. The VBGF is most commonly used as a descriptive model of size-at-age data (Essington et al., 2001). Nevertheless, Eq. (1.1) describes the relationship between age and mean length of a population, whereas the variability among individuals of the same age (e.g. the variance or even the distribution of each cohort) is not included.

The popular assumption of Gaussianity (Imsland et al., 1998) is clearly a first (rough) approximation in this direction. A natural approach to the problem of determining the appropriate form of the probability distribution for a population at a given time t is to model first the growth process of the individuals (individual-based models, IBM). Nowadays, in both ecological (Arino et al., 2004), evolutionary (Conover and Munch, 2002; Ernande et al., 2004) and management (Caswell, 2001) contexts, one of the challenges of the researcher is to model how the size of an individual changes in time and to deduce from the growth model which kind of probability distribution models the size of fish at a given age (Lv and Pitchford, 2007; Fujiwara et al., 2004).

A suitable model of growth should account for both individual and environmental variability. In fish, as in other animals, the first source of variability is rooted in the physiological processes and is the net result of two opposing processes, catabolism and anabolism (von Bertalanffy, 1938). The inter-individual variability in growth is the result of several internal (genetic) and external (environmental) factors which affect these physiological processes. In fact, whilst each individual is born with a personal genetic architecture which primarily determines his growth profile, a number of physical and biological factors, such as water

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* Corresponding author. Tel.: +390672595974; fax: +390672595965.
E-mail address: Tommaso.Russo@Uniroma2.it (T. Russo).

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temperature (Sumpter, 1992), dissolved oxygen (Brett, 1979), photoperiod (Imsland et al., 2002), and the availability of appropriate food sources (Rilling and Houde, 1999), have been shown to affect growth rates. In order to take into account these aspects as well as individual variability, a class of IBM was developed (Lv and Pitchford, 2007; Sainsbury, 1980; Mulligan and Leaman, 1992; Wang and Thomas, 2003; Imsland et al., 2002; Wang, 1999; Gudmundsson, 2005).

These models can be classified into two main categories. The first comprises those which consider the inter-individual variability as a stochastic factor to be added to the general growth curve of the population. The distribution of this factor is the same for all the individuals. In the most recent approaches of this kind (Gudmundsson, 2005; Lv and Pitchford, 2007; Wang, 1999) some individual-based stochastic models of growth are proposed using a stochastic differential equations. These models take the general form

$$dL_t = f(L_t, t) + \alpha(L_t, t)\, dB(t). \tag{1.2}$$

Here L_t is the size at time t, $f(L_t, t)$ characterizes the deterministic intrinsic growth (drift coefficient) of the individual (the same for all individuals); $\alpha(L_t, t)$ gives the magnitude of the random fluctuations (diffusion coefficient) and $B(t)$ is a standard Brownian motion, or Wiener process, which is commonly used to model a variety of background and environmental fluctuations in physical, financial and biological contexts (see, e.g. Karlin and Taylor, 1981).

The stochastic component of these models is intended to account for both the environment and the inter-individual variability. It should be stressed, however, that (as already remarked in Gudmundsson, 2005) the solution of an equation as Eq. (1.2) cannot be monotonically increasing and therefore appears to be unsuitable to model the evolution of the size of an individual. Stochastic models like the one of Eq. (1.2) are conversely well suited in order to model quantities, as prices in financial markets, that are characterized by an oscillating and therefore non-monotonic behaviour. This aspect seems to be a drawback for a growth model of several animals like fish. In fact, for fish and other vertebrates, the physiological mechanism of growth in length (i.e. the addition of bone material to the axil unit of the skeleton that is the vertebra) leads to a pattern in which the size of an individual is necessarily increasing in time (Weatherley and Gill, 1987). Let us point out that there exist no Gaussian process which is increasing. Therefore, modelling size variability through an individual growth process cannot give rise to a Gaussian distribution.

Closely related to the models (Eq. (1.2)) are those introduced in Gudmundsson (2005) where it is the derivative of the growth process that is the solution of a stochastic equation. It is possible in this way to obtain a stochastic process that is increasing. These models are interesting and deserve to be tried by testing against real data. Remark, however, that the mean size at time t of a population following such a model does not follow a VBGF.

The second category of stochastic models suggested so far comprises non-deterministic models in which the individuals of a fish population have different parameters of the VBGF. In this way, each individual has its own triplet (L_∞, t_0, k), which is retained throughout its life (Sainsbury, 1980). Considering the length to age relationship, the length X_t at age t of the ith individual with the parameters triple $(L_i, t_{0,i}, k_i)$ is given by

$$X_{t,i} = L_i\left(1 - \mathrm{e}^{-k_i(t+t_{0,i})}\right). \tag{1.3}$$

This model displays a monotonic behaviour and considers the inter-individual variability of growth parameters, but does not account for the randomness coming from the environment, which can be seen as a limitation of the model.

Finally, it should be considered that individual growth is a complex energetic process. Individual length increases only when enough energy from food is available for growth. On the other hand the lack of food does not usually lead to a reduction in length, because organisms can lose body mass without shrinking in length (Kooijman, 2000) which also because of the presence of a skeleton. Energy may also be allocated to storage for future use, producing “memory” in growth dynamics. Individual organisms encounter and ingest food, which is then assimilated. Assimilated food is transformed into reserve material such as protein and fat. A fixed fraction of the energy from the reserve is used for both metabolic maintenance and growth, and the rest is used for reproduction. Looking at the length of an individual, we suggest that this process determines a pattern in which periods of no growth (determined by scant energy inlet) are separated by periods of growth. If the periods of growth are short, the growth process could be well described by a model allowing for discontinuities, i.e. for instantaneous increases of the length (jumps). This idea is consistent with several observations reported for fish in general and for the species we are going to study (Hinrichsen et al., 2007).

In this paper we introduce two classes of stochastic models of growth that attempt to overcome the drawbacks pointed out above. The main idea developed in this paper is to model the growth process as the solution of a stochastic equation of the form

$$dX_t = (L_\infty - X_{t-})\, dZ_t,$$

where $(Z_t)_t$ is a *subordinator*. These are a class of stochastic processes that are strictly increasing and the solution $(X_t)_t$ turns out to be increasing also. These models enjoy a certain number of desirable features, namely

- they take into account both the individual and the environmental sources of randomness;
- they are increasing;
- the mean size at time t follows a VBGF.

In Section 2 we make a quick review on the topics of subordinators upon which our models are built. In Sections 3 and 4 some models are developed, attempting to answer to the points exposed above. Finally in Section 6 we apply the proposed models to a large set of length-at-age data of Atlantic herring *Clupea harengus*, presented in Section 5.

2. Subordinators

A *subordinator* is a stochastic process $(Z_t)_t$ such that

- $Z_0 = 0$;
- its paths are right continuous and increasing almost surely;
- has independent and stationary increments.

This means in particular that the distribution of $Z_{t+h} - Z_t$ is independent of t for every $h \geqslant 0$ and that $Z_t - Z_s$ and $Z_v - Z_u$ are independent r.v.'s for $u < v \leqslant s < t$. Also the increments $Z_{t+h} - Z_t$ must be stationary, in the sense that their distribution depends on h only and not on t. The characterization of such processes (that are particular instances of Lévy processes) has received much attention in time and it is characterized in terms of the Laplace transform of Z_t. It is immediate that if

$$M_t(\theta) = \mathrm{E}(\mathrm{e}^{-\theta Z_t}), \quad \theta \geqslant 0 \tag{2.1}$$

then M is of the form

$$M_t(\theta) = \mathrm{e}^{t\phi(\theta)}, \tag{2.2}$$