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

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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.

Key words: Individual-based models, Subordinators, Fish growth, *Clupea harengus*, Fisheries

1 Introduction

The modeling of growth and the analysis of intra-population pattern of size variability through time are 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 & 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

$$x_t = L_\infty(1 - e^{-k(t+t_0)}) \quad (1.1)$$

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, equation (1.1) describes the relationship between age and mean length of a

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17 population, whereas the variability among individuals of the same age (e.g.
18 the variance or even the distribution of each cohort) is not included.

19 The popular assumption of gaussianity (Imsland *et al.*, 1998) is clearly a first
20 (rough) approximation in this direction. A natural approach to the problem
21 of determining the appropriate form of the probability distribution for a
22 population at a given time t is to model first the growth process of the
23 individuals (individual based models, IBM). Nowadays, both in ecological
24 (Arino *et al.*, 2004), evolutionary (Conover & Munch, 2002; Ernande *et al.*,
25 2004) and management (Caswell, 2001) contexts, one of the challenges of the
26 researcher is to model how the size of an individual changes in time and
27 deduce from the growth model which kind of probability distribution models
28 the size of fish at a given age (Lv & Pitchford, 2007; Fujiwara *et al.*, 2004).

29 A suitable model of growth should account for both individual and
30 environmental variability. In fish, as in other animals, the first source of
31 variability is rooted in the physiological processes and is the net result of two
32 opposing processes, catabolism and anabolism (von Bertalanffy, 1938). The
33 inter-individual variability in growth is the result of several internal (genetic)
34 and external (environmental) factors which affect these physiological
35 processes. In fact, while each individual is born with a personal genetic
36 architecture which primarily determines his growth profile, a number of
37 physical and biological factors, such as water temperature (Sumpter, 1992),
38 dissolved oxygen (Brett, 1979), photoperiod (Imsland *et al.*, 2002), and the
39 availability of appropriate food sources (Rilling & Houde, 1999), have been
40 shown to affect growth rates. In order to take into account these aspects as
41 well as individual variability, a class of individually based model (IBM) was
42 developed (Lv & Pitchford, 2007; Sainsbury, 1980; Mulligan & Leaman,

1992; Wang & 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 & Pitchford, 2007; Wang, 1999) some individual-based stochastic models of growth are proposed using a stochastic differential equations. These models take the general form:

$$dL_t = f(L_t, t) + \alpha(L_t, t) dB(t) \quad (1.2)$$

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 Karlin & Taylor (1981) e.g.

The stochastic component of these models is intended to account both for 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 (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 (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. 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 & Gill, 1987). Let us point out that there exist no Gaussian process which is increasing. Therefore, modeling size variability through an individual growth process, can not give rise to a Gaussian distribution.

Closely related to the models (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) , that is retained throughout its life (Sainsbury, 1980). Considering the length to age relationship, the length X_t at age t of the i -th individual with the parameters triple $(L_i, t_{0,i}, k_i)$ is given by:

$$X_{t,i} = L_i(1 - e^{-k_i(t+t_{0,i})}) \quad (1.3)$$

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 lack of food does not usually lead to a reduction in length, because organisms can lose body mass without shrinking in length (Kooijman, 2000) 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 environmental sources of randomness;
- they are increasing.
- the mean size at time t follows a VBGF.

In §2 we make a quick review on the topics of subordinators upon which our models are built. In §3 and §4 some models are developed, attempting to answer to the points exposed above. Finally in §6 we apply the proposed models to a large set of length-at-age data of Atlantic herring *Clupea harengus*, presented in §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 $h \geq 0$ and that $Z_t - Z_s$ and $Z_v - Z_u$ are independent r.v.'s for $u < v \leq s < t$. 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

135 terms of the Laplace transform of Z_t . It is immediate that if

$$M_t(\theta) = E(e^{-\theta Z_t}), \quad \theta \geq 0 \quad (2.4)$$

136 then M is of the form

$$M_t(\theta) = e^{t\phi(\theta)} \quad (2.5)$$

137 where the exponent ϕ is characterized by the Lévy-Khintchin formula (see,
138 for the subjects developed in this section and in the next ones
139 Cont & Tankov 2004 and Sato 1999 e.g.). More precisely, the
140 Lévy-Khintchin formula for subordinators states that

$$\phi(\theta) = -\theta\gamma + \int_0^{+\infty} (e^{-\theta x} - 1) \nu(dx)$$

141 where $\gamma \geq 0$ and ν , the *Lévy measure*, is a positive measure on $\mathbb{R}^+$ such that

$$\int_0^{+\infty} \frac{x}{1+x} \nu(dx) < +\infty \quad (2.6)$$

142 Intuitively a subordinator increases as the superposition of a deterministic
143 evolution $t \rightarrow \gamma t$ and of a stochastic process which only makes jumps. These
144 are made at times governed by a Poisson process. More precisely, if
145 $0 < a < b$, then $\nu([a, b])$ is the intensity of the Poisson process of the jumps
146 whose size is larger than a and smaller than b . This means that if t is the
147 (random) time at which the jump occurs, then the path has, at t , a left limit
148 X_{t-} and a right limit X_{t+} that are different, with $X_{t-} < X_{t+}$. For our
149 purposes we shall therefore be much interested in subordinators whose Lévy
150 measure is large to near 0 and gives a small mass only away from 0. The
151 resulting process would hence be characterized by many very small jumps.

152 As every Lévy process, the independence and stationarity properties of the
153 increments implies that if Z_t has a finite mean, then

$$E(Z_t) = \mu t$$

154 for some real number μ and if it has a finite variance then

$$\text{Var}(Z_t) = \sigma^2 t$$

155 for some $\sigma^2 \geq 0$.

156 It is not possible for a general Lévy measure to compute explicitly the
157 Laplace transform and/or the density at time t of the associated
158 subordinator. The next examples introduce some families of subordinators of
159 interest for which these feature can be determined.

160 • the Gamma process, where the distribution of Z_t follows a $\Gamma(\alpha t, \lambda)$
161 distribution. Recall that such a distribution has a density

$$f(x) = \frac{\lambda^{\alpha t}}{\Gamma(\alpha t)} x^{\alpha t - 1} e^{-\lambda x}, \quad x > 0$$

162 and $f(x) = 0$ for $x \leq 0$. Of course the increment $Z_t - Z_s$, having the same
163 distribution as Z_{t-s} , has a $\Gamma(\alpha(t-s), \lambda)$ distribution. Its Laplace transform is

$$M_t(\theta) = \left(\frac{\lambda}{\lambda + \theta} \right)^{\alpha t} \quad (2.7)$$

164 so that $\phi(\theta) = -\alpha \log \frac{\lambda}{\lambda + \theta}$. From well-known properties of the $\Gamma(\alpha t, \lambda)$
165 distribution the statistical indices of interest of a Gamma process are:
166 mean = $\alpha t / \lambda$, variance = $\alpha t / \lambda^2$, skewness = $2 / \sqrt{\alpha t}$ and kurtosis =

167 $3 + 6/(\alpha t)$.

168 Here the Lévy measure is

$$\nu(dy) = \frac{\alpha}{y} e^{-\lambda y} dy.$$

169 This process therefore gives a high intensity to small jumps (see Fig 1).

170 • The *inverse Gaussian processes*, where Z_t is defined as the first time at
171 which a process of the form $\sqrt{\rho}B_s + bs$ crosses level t . Here $(B_t)_t$ denotes a
172 standard Brownian motion and $\rho, b > 0$. Its density at time t is, for $x > 0$,

$$f_t(x) = \frac{te^{bt/\rho}}{(2\pi\rho)^{1/2}x^{3/2}} \exp\left(-\frac{b^2}{2\rho}x - \frac{t^2}{2\rho x}\right).$$

173 It depends on the positive parameters b, ρ . Its Laplace transform at time t is

$$M_t(\theta) = \exp\left(-t\left(\sqrt{\frac{b^2}{\rho^2} + \frac{2\theta}{\rho}} - \frac{b}{\rho}\right)\right),$$

174 from which one can derive the expression of the statistical indices of interest:

175 mean = t/b , variance = $\rho t/b^3$, skewness = $3\sqrt{\rho/(tb)}$ and kurtosis =
176 $3 + 15\rho/(tb)$.

177 The Lévy measure is

$$\nu(dy) = \frac{1}{\sqrt{2\pi\rho y^3}} e^{-\frac{1}{2\rho}b^2 y} dy. \quad (2.8)$$

178 We stress that both the Gamma and the inverse Gaussian process have a
179 Lévy measure that gives much weight to small jumps and that decreases fast
180 at infinity.

181 • The α -stable process, $0 < \alpha < 1$ whose Laplace transform is

$$M_t(\theta) = e^{-c\theta^\alpha t}.$$

182 For these processes an explicit expression for the density does not exist,

183 unless $\alpha = \frac{1}{2}$. In this case, for $c = \sqrt{2}$, the density is, for $x > 0$,

$$f(x) = \frac{t}{(2\pi)^{1/2}x^{3/2}} e^{-\frac{t^2}{2x}}.$$

184 Notice that, as $x \rightarrow +\infty$ the density decreases very slowly and, in particular,

185 both expectation and variance are infinite. Also the Lévy measure decreases

186 very slowly at infinity, therefore allowing very large jumps. We shall see that

187 this model is not well suited for the growth phenomena of interest and we

188 mention it only for reasons of completeness.

189 To the previous examples one should add the deterministic increasing

190 process: $Z_t = \gamma t$. Recall also that the sum of independent subordinators is a

191 subordinator itself.

192 3 Modeling by time change

193 A first growth model using subordinators can be obtained by time change.

194 We simply consider that the size of the fish X_t at time t is given by

$$X_t = Z_{A_t}$$

195 where Z is the subordinator and A is the von Bertalanffy type function

$$A_t = (1 - e^{-k(t+t_0)}).$$

196 If the subordinator Z_t has finite mean, then for some real number μ

$$E(X_t) = \mu (1 - e^{-k(t+t_0)})$$

197 and the means follow therefore a VBGF, where μ plays the role of L_∞ (recall
198 that $\mu = E(Z_1)$).

199 If in particular Z is a Gamma process, then $\mu = \frac{\alpha}{\lambda}$. It is also immediate that,
200 if Z_t has finite variance,

$$\text{Var}(X_t) = \sigma^2 (1 - e^{-k(t+t_0)}) \quad (3.9)$$

201 for some $\sigma^2 > 0$ ($\sigma^2 = \frac{\alpha}{\lambda^2}$ if Z is a Gamma process). Recall that the variance
202 is always increasing in t . This fact makes that the models obtained by time
203 change of a subordinator are rather rigid and are in particular unable to
204 account for a non monotonic behaviour of the variance, as is often observed
205 in data.

206 4 Modeling by Doléans exponential

207 A more interesting model of growth is given by the process $(X_t)_t$ which is
 208 obtained as the solution of the stochastic equation

$$\begin{aligned} dX_t &= (L_\infty - X_{t-}) dZ_t \\ X_{-t_0} &= 0 \end{aligned} \tag{4.10}$$

209 where $(Z_t)_t$ is a subordinator. Here $-t_0$ denotes the time of conception, at
 210 which the size must be considered equal to 0. If the subordinator Z has a
 211 drift γ equal to 0, the solution of (4.10) is a process that remains constant
 212 between the jumps of Z , whereas it has an increment of size

$$(L_\infty - X_{t-}) \Delta Z_t$$

213 whenever Z has a jump of size ΔZ_t . The quantity X_{t-} denotes the value of
 214 X just before the jump that occurs at time t . If we define $Y_t = L_\infty - X_t$,
 215 then Y is the solution of

$$\begin{aligned} dY_t &= -Y_{t-} dZ_t \\ Y_{-t_0} &= L_\infty . \end{aligned} \tag{4.11}$$

216 Therefore Y is equal to the Doléans exponential of the Lévy process $-Z$
 217 multiplied by L_∞ . The Doléans exponential of the Lévy process is a subject
 218 that has received much attention and it is possible to derive an explicit
 219 solution of (4.11), at least if one makes the assumption that the process Z
 220 cannot make jumps larger than 1 (which is a quite reasonable assumption, in

our case). Under this assumption the solution of (4.11) is

$$Y_t = L_\infty e^{-\tilde{Z}_{t+t_0}} \quad (4.12)$$

where $\tilde{Z}$ is another subordinator whose Lévy measure $\tilde{\nu}$ and drift $\tilde{\gamma}$ are obtained from ν and γ in an explicit way. More precisely $\tilde{\nu}$ is the image of ν through the application $x \rightarrow \log(1+x)$ and $\tilde{\gamma} = \gamma$. The solution of (4.10) is therefore

$$X_t = L_\infty (1 - e^{-\tilde{Z}_{t+t_0}}). \quad (4.13)$$

It is easy to compute the mean $E(X_t)$, as the quantity $E(e^{-\tilde{Z}_{t+t_0}})$ is the Laplace transform at $\theta = 1$ of the r.v. Z_{t+t_0} , which is easy to compute thanks to (2.4) and (2.5):

$$E(X_t) = L_\infty (1 - e^{-(t+t_0)\tilde{\phi}(1)}). \quad (4.14)$$

Hence also for this model whatever the subordinator that is chosen (provided its Lévy measure vanishes outside $]0, 1]$), the mean of the solution of (4.10) follows a von Bertalanffy-type equation.

Note 4.1 Recall that the VBGF (1.1) is the solution of equation (4.10) when Z is the deterministic subordinator $Z_t = kt$. Therefore (4.10) appears as a natural stochastic extension of the VBGF.

Remark also that some models already present in the literature are particular instances of (4.10). It is the case of the model (3.4) of Lv & Pitchford (2007) where the authors actually consider $Z_t = rt + \sigma B_t$. We point out again that the solution to (4.10) in this case does not have paths which are monotonically increasing.

240 The solution (4.13) however has a drawback as a growth model because
 241 $X_t \rightarrow L_\infty$ as $t \rightarrow +\infty$ (unless $Z_t \equiv 0$). This implies that $\text{Var}(X_t) \rightarrow 0$ as
 242 $t \rightarrow +\infty$, which is not realistic, as it would imply that all individuals should
 243 reach the same limiting size as t increases. In order to overcome this problem
 244 it seems natural to assume that the extremal size L_∞ is itself a random
 245 variable, thus accounting for the individual variability. In this way the two
 246 sources of randomness, L_∞ and $(Z_t)_t$, appearing in equation (4.10) have the
 247 meaning of modeling the random individual variability and the
 248 environmental randomness respectively. It is therefore natural to assume
 249 that L_∞ and $(Z_t)_t$ are independent. In this case formula (4.14) remains valid
 250 if one replaces L_∞ by $E(L_\infty)$. Therefore the expectation $E(X_t)$ still follows a
 251 von Bertalanffy-type pattern as in (4.14), but with L_∞ replaced by $E(L_\infty)$.
 252 Similarly it is easy to compute the variance which is given by

$$\begin{aligned} \text{Var}(X_t) &= \text{Var}(1 - e^{-\tilde{Z}_{t+t_0}})E[L_\infty^2] + \text{Var}(L_\infty^2)E[1 - e^{-\tilde{Z}_{t+t_0}}]^2 = \\ &= \left(e^{-(t+t_0)\tilde{\phi}(2)} - e^{-2(t+t_0)\tilde{\phi}(1)}\right)E[L_\infty^2] + \text{Var}(L_\infty^2)\left(1 - e^{-(t+t_0)\tilde{\phi}(1)}\right)^2. \end{aligned} \quad (4.15)$$

253 Notice that $\text{Var}(X_t)$ appears as the sum of two terms. As both $\tilde{\phi}(1)$ and $\tilde{\phi}(2)$
 254 are positive, the first term vanishes at $-t_0$ and at $+\infty$ and it easy to see that
 255 (unless $Z_t \equiv 0$) it increases at first and then decreases. The second one
 256 conversely is increasing in t . Therefore the variance of X_t , according to
 257 different values of the parameters, can exhibit two possible behaviours:

- 258 • increasing or
- 259 • first increasing and then decreasing.

260 See Figure 2 for an illustration of this typical behaviour.

261 The non monotonic behaviour of the variance is an interesting feature that is
 262 enjoyed also by some of the models proposed by Gudmundsson, 2005 and
 263 Lv & Pitchford, 2007. This is not surprising as the computation above only
 264 makes use of the fact that $(X_t)_t$ is the solution of equation (4.10) with a
 265 driving process $(Z_t)_t$ which is a Lévy process, possibly a Brownian motion as
 266 it happens to be the case for the models of the authors above.

267 **Note 4.2** In §6 we adapt the models of this section and of §3 to a
 268 population of herrings. It is fair however to point out a limitation that arises
 269 when trying to model real populations with processes driven by
 270 subordinators. Recall that the driving subordinator is meant to model the
 271 randomness of the growth process arising from the environment. The
 272 assumption of independence and stationarity of the increments of the
 273 subordinator implies the assumption that the environment remains stable
 274 and stationary in time, which is a feature that can be expected to hold in
 275 real world only for a short span of time, as the effect of season and of other
 276 sources of modification of the natural habitat should introduce a
 277 time-dependent effect. It is clear however that more realistic models would
 278 be far more complicated and, possibly, intractable in practice. The same
 279 observation, by the way, applies to the VBGF, which is an equation that is
 280 derived under the assumption of stationarity of the environment.

281 In the rest of this section we give more details in two particular cases,
 282 making assumptions on Z that imply that $\tilde{Z}$ is either a Gamma or an inverse
 283 Gaussian process.

284 Assume that the Lévy measure ν of Z has a density h with respect to the
285 Lebesgue measure. h must be ≥ 0 , must vanish on $[1, +\infty[$ and be such that

$$\int_0^1 y h(y) dy < +\infty$$

286 Then $-Z$ has a drift $= -\gamma$ and a Lévy measure $\bar{\nu}$ given by the density

$$\bar{h}(y) = h(-y)$$

287 The image of the measure $\bar{h}(y) dy$ by $y \rightarrow \log(1 + y)$ is

$$\tilde{h}(y) = e^{-y} h(1 - e^{-y})$$

288 **Example 4.3** (The Gamma process) Let us assume that

$$h(y) = \frac{\alpha}{-\log(1 - y)} (1 - y)^{\lambda-1} \quad (4.16)$$

289 for $0 < y \leq 1$ and $h(y) = 0$ for $y > 1$, where $\alpha > 0$, $\lambda > 0$. With this choice
290 we obtain

$$\tilde{h}(y) = \frac{\alpha}{y} e^{-\lambda y}$$

291 which is the Lévy measure of a Gamma process. Hence if we choose a driving
292 subordinator Z with a Lévy measure as in (4.16) and drift γ , the solution of
293 (4.10) is

$$X_t = L_\infty (1 - e^{-\gamma t - \tilde{Z}_{t+t_0}}) \quad (4.17)$$

294 where $\tilde{Z}$ is a Gamma process with parameters α and λ and drift γ . Thanks
295 to (4.10) and (2.7), for this model the mean is equal to

$$E(X_t) = E(L_\infty) \left(1 - e^{-\gamma(t+t_0)} \left(\frac{\lambda}{\lambda + 1} \right)^{\alpha(t+t_0)} \right) \quad (4.18)$$

which, as already noted, is a von Bertalanffy equation with
 $k = \gamma + \alpha \log \frac{\lambda+1}{\lambda}$. The variance of X_t is also easily computed using (4.15):

$$\begin{aligned} \text{Var}(X_t) = & \mathbb{E}[L_\infty^2] e^{-2\gamma(t+t_0)} \left[\left(\frac{\lambda}{\lambda+2} \right)^{\alpha(t+t_0)} - \left(\frac{\lambda}{\lambda+1} \right)^{2\alpha(t+t_0)} \right] + \\ & + \text{Var}(L_\infty) \left[1 - e^{\gamma(t+t_0)} \left(\frac{\lambda}{\lambda+1} \right)^{\alpha(t+t_0)} \right]^2. \end{aligned} \quad (4.19)$$

It is also possible to compute the density of X_t , conditioned to the value of
 $L_\infty = l$, which is given by

$$f(x) = \frac{\lambda^{\alpha(t+t_0)} (l-x)^{\lambda-1}}{\Gamma(\alpha(t+t_0)) l^\lambda} \left(-\log(1 - \frac{x}{l}) - \gamma(t+t_0) \right)^{\alpha(t+t_0)-1} e^{\lambda\gamma(t+t_0)} \quad (4.20)$$

for $l(1 - e^{-\gamma(t+t_0)}) \leq x \leq l$ and $f(x) = 0$ otherwise. The graph of this density
 for different values of t is produced in Figure 3. See in Figure 4 the graph of
 some simulated paths of $(X_t)_t$ with $\gamma = 0$.

Example 4.4 (The inverse Gaussian process) Let us assume that Z is a
 Levy process such that $\tilde{Z}$ is an inverse Gaussian process with drift γ . If the
 Lévy measure of Z has a density

$$h(x) = \frac{1}{\sqrt{2\pi\rho}(-\log(1-x))^{3/2}} (1-x)^{\frac{b^2}{2\rho}-1}$$

for $0 < x < 1$ and $h(x) = 0$ elsewhere, then it turns out that $\tilde{Z}$ is an inverse
 Gaussian process with parameters b and ρ . The density of
 $X_t = L_\infty(1 - e^{-\tilde{Z}_t - \gamma t})$ given $L_\infty = l$ is straightforward to compute and is

$$f_t(x) = \frac{te^{bt/\rho}}{\sqrt{2\pi\rho}} (-\log(1 - \frac{x}{l}))^{-3/2} (1 - \frac{x}{l})^{\frac{b^2}{2\rho}-1} \exp\left(\frac{t^2\rho}{2\log(1 - \frac{x}{l})}\right)$$

for $0 < x < l$ and $f_t(x) = 0$ otherwise.

One could also think of $\tilde{Z}$ as a stable process with exponent $\alpha = \frac{1}{2}$. This choice however does not seem really suitable. Indeed in this case it is also possible to compute the density, as the same type of computation produces in this case the density, conditional on $L_\infty = l$,

$$g_t(x) = \frac{t + t_0}{\sqrt{2\pi}(l - x)(\log \frac{l}{l-x})^{3/2}} \exp\left(-\frac{(t + t_0)^2}{2 \log \frac{l}{l-x}}\right), \quad 0 < x < l.$$

(with $\gamma = 0$). The expression of this density suggests that the use of stable subordinators is inappropriate in order to model fish growth, as $g(x) \rightarrow +\infty$ as $x \rightarrow l-$, for every value of t .

The model based on the Doléans exponential (4.10) appears to enjoy many interesting features. It is fair however to point out that in order to take advantage of it there remains the question of determining an appropriate distribution for the maximal length L_∞ . It also appears difficult to find a distribution such that the density distribution of the length of the individuals of a given time t , $L_\infty(1 - e^{-Z_{t+t_0}})$ has an explicit analytic expression. This density can be computed numerically, but it may be impossible to use of statistical methods based on maximum likelihood.

The question of determining a good candidate of distribution has been already tackled in (Sainsbury, 1980), where the author suggested a Gamma distribution.

5 The Dataset

The data used in this study were collected as part of the EU FP5 project “HERGEN” (Mariani *et al.*, 2005; Ruzzante *et al.*, 2006), and include a

homogeneous collection of genetically and phenotypically characterized North Sea Autumn Spawning herring (*Clupea harengus* L., 1758), from ICES areas zones IVa, IVb and IVc. Herring is the dominant converter of zooplankton production, using the biomass of copepods, mysids, euphausiids in the pelagic environment of the northern hemisphere (Winters & Wheeler, 1987). Additionally, herring is a central prey item for higher trophic levels. The spawning period of this species in the western North Sea is September/October.

The samples were collected east of the Shetland Islands in July 2005. At that moment, fish were located in that area to feed (summer feeding aggregation). Aging was performed by counting the otolith (sagitta) winter rings, following standard procedures (Ruzzante *et al.*, 2006; AA.VV, 2007). This method was validated and tested for reliability following the procedure reported in Beverton *et al.* (2004). The dataset is composed by 1255 specimens belonging to 7 cohorts. The abundances and the ages of these cohorts are showed in Table 1. The values of the empirical means and variances of the cohorts can be found in Fig 5.

6 Analysis of the herring dataset

In order to apply the models developed in §3 and §4 to the analysis of a dataset as the herring one described in the previous section, one is confronted with two kind of problems.

The first one is the determination of the appropriate driving subordinator. Actually subordinators form a large family, every Lévy measure on $\mathbb{R}^+$ satisfying (2.6) being associated to a corresponding subordinator. This is

therefore a non parametric problem and it appears very difficult to determine this Lévy measure starting from data in the form of cohorts, as is the case for the herring dataset.

The second order of problems comes from the fact that these models are to be considered only approximatively correct, as they do not take into account the time variability of the environment (see Note 4.2).

In this section we produce the results obtained fitting the models of §3 and 4 to the herring dataset. In both cases we decided to work with the Gamma model, as it seemed to give better results than the inverse Gaussian.

In order to have a benchmark for the analysis of the dataset, we shall first adapt a normal Gaussian model inside each cohort. This is the default choice in literature (Immsland *et al.*, 1998). Given the age t_i , the length X_{t_i} is assumed to be normally distributed with mean $L_\infty(1 - e^{-k(t_i+t_0)})$ and variance σ_i^2 (different cohorts are allowed to have different variances). This model requires therefore a number of parameters that is equal to 3+the number of cohorts.

It is worth noting that this is not a mixture model, as we are able to assign every individual to its class. Recall also that, as stated in the introduction, this is not a Individual Based Model.

The normal and time change models have been estimated by means of maximum likelihood, which appears to be the most natural method for them. As already pointed out in §4, for the Doléans exponential model, which is the most promising, the maximum likelihood method is inapplicable, as the distribution of the maximal size L_∞ is not known. We therefore resorted to the least squares method in order to fit the moments.

380 The estimates obtained with different models are shown in Table 2.

381 It is apparent that the normal model has a good agreement with the data,
382 which is not surprising, given also the availability of many parameters.

383 6.1 Time change model

384 As already hinted in §3 this kind of models shows a certain rigidity. We give
385 the estimates obtained using it for completeness sake only. Assuming that
386 the lengths at time t_i follow a $\Gamma(\alpha(1 - e^{-k(t_i+t_0)}), \lambda)$ distribution, we have a
387 model with 4 parameters (whatever the number of cohorts). The estimated
388 values are $\alpha = 388.2$, $\lambda = 1.33$, $k = 0.64$ and $t_0 = 0.047$. From this we deduce
389 $\hat{L}_\infty$ as the ratio $\hat{\alpha}/\hat{\lambda}$ (see Table 2). Estimates of the means and variances are
390 obtained using (3.9).

391 Notice that the estimated means are very close to the empirical means (with
392 the exception of cohort 1). However it is clear that this model cannot
393 accommodate the variances. Recall that for this model the variances are
394 necessarily increasing with time, at a difference with the behaviour of the
395 empirical variances.

396 As already mentioned above, the model based on time change is a
397 particularly parsimonious explanation of the data in terms of number of
398 parameters, but has limited capacities of catching some relevant features.

399 6.2 Doléans exponential

400 We tried a model based on the solution of (4.10) with respect to a Gamma
401 process, as in Example 4.3.

402 According to this model, the density of the observations follows a
403 distribution, given $L_\infty = l$, that is given in (4.20). Noting that the mean
404 values of the lengths of the different cohorts must lie on the VBGF, we
405 decided to perform a two-stage method of moments, in which, at first, the
406 empirical means are interpolated by a VBGF function (1.1), therefore
407 estimating the parameters $E(L_\infty)$, k and t_0 . In the second stage, we
408 interpolated the empirical variances with the function (4.19). In this way we
409 obtained estimates of α , λ , γ together with an estimate of $\sigma_{L_\infty}^2 = \text{Var}(L_\infty)$.
410 Recall that the quantities k and α , λ , γ are related by the constraint
411 $k = \gamma + \alpha \log \frac{\lambda+1}{\lambda}$. For both stages we used a least squares method in order
412 to fit the moments.

413 See Fig 5 for the graph of the fitted von Bertalanffy function and the
414 empirical means with error bars.

415 This method produces an estimate of the mean and variance of L_∞ without
416 assuming any distribution for L_∞ . The estimates are $\alpha = 1.3$, $\lambda = 15$,
417 $\gamma = 0.55$, $k = 0.63$, $t_0 = 0.072$, $E(L_\infty) = 297.3$ and $\sigma_{L_\infty}^2 = 160$. Finally, in
418 order to obtain a concrete and visually appreciable estimate of the density of
419 each cohort, we computed it numerically assuming for L_∞ a Gamma
420 distribution having parameters matching the estimated mean and variance,
421 that is with parameters $\alpha_0 = 552.34$ and $\lambda_0 = 1.86$. Figure 6 produces a
422 comparison between the density obtained as described above from the model

and an empirical density, produced from the data with a usual kernel estimator. Taking into account the limited number of parameters employed by this model one can appreciate the nice fit for some of the cohorts. Discrepancies can be found for the first two cohorts and for the sixth one. For the fifth one there is a evident discrepancy: notice however that, as pointed out in Fig 5, also the estimated VBFG curve that fits the mean of this fifth cohort. At this point one should keep in mind Note 4.2.

7 Discussion

Although several stochastic model are available in the literature in order to compute the time evolution of the distribution of the size of a population, a certain number of drawbacks still remain, leading to the need of a more appropriate formulation that is able to take into account some key aspects of animal growth.

These aspects basically concern the inclusion of the different sources of variability in growth rate among individuals, which directly determine the size density observed at different ages, and the property of the growth process of being increasing. In this work we developed two models based on the use of subordinators as driving processes. Our aim was to provide a new stochastic model, mainly of theoretical interest for the description of the growth process for a large class of organisms. It turns out that one of them, the model based on the Doléans exponential giving rise to a Gamma process, is also able to produce an appreciable fit with the data. In particular it is able to reproduce the non monotonic trend of the variance, that is the measure of intra-cohort variability of size. This is an important feature: a

447 reduction of the demographic variance starting at some time is often
 448 observed in data (Gudmundsson, 2005 e.g.).

449 In general, the variability in individual size increases within the same cohort
 450 through time when the individual growth rate is positively correlated with
 451 itself in time (Gudmundsson, 2005). This phenomenon is called “growth
 452 depensation”.

453 Conversely, a reduction of the cohort variance (the so called “growth
 454 compensation”) has been up to now explained with the fact that survival of
 455 individuals are not independent and identically distributed (Kendall & Fox,
 456 2002). In other words, there needs to be some systematic structure in the
 457 population. Common biological mechanisms that can produce a reduction of
 458 demographic variance are contest competition (including territoriality),
 459 long-lived individuals with lifetime demographic traits (“individual
 460 heterogeneity”), maternally imposed variation, and directional or balancing
 461 selection.

462 Observe however that our model explains this typical behaviour of the
 463 variance without introducing an explicit selection mechanism related to some
 464 size-dependent mortality. By this we do not claim that such a mechanism
 465 does not exist (and we think that it might be natural to devise a more
 466 sophisticated model including this feature), but simply that it is not necessary
 467 in order to explain the observed behavior of the empirical variances.

468 The possibility to model and predict this aspect of fish growth seems to be of
 469 great importance in both theoretical studies and fishery management
 470 applications. This is particularly true if referred to the increasing use of
 471 measurement of the growth pattern of organisms (like fish) as an ecological

indicator (Bennett *et al.*, 1995). Further, assessment of growth pattern,
 combined with other measurement of physiological condition, have the
 potential to yield information on the history of environmental stress (e.g.
 from contaminants) or selective pressures (e.g. fisheries) and adaptation to
 environmental change (Jorgensen *et al.*, 2007). In fact, statistical analyses of
 long-term data from some exploited fish stocks have revealed evolutionary
 changes in reaction norms (Ernande *et al.*, 2004). Accuracy of the growth
 model at the basis of these analyses obviously affect the results, so that the
 development of sound approach to model and predict size distribution is a
 main target.

A future direction will concern the assessment of the effect of the aging error
 on the estimates obtained using our model. Even if the aging method is
 reliable, it seems that errors in aging young cohorts can significantly affect
 the estimates. This is due to the fact that both VBGF and the variance
 function converge with age.

The present work represent a first attempt to apply the Lévy processes to
 the subject. We think that these and the ideas developed in this paper can
 be adapted to introduce stochasticity into more complex models of growth
 (see Edwards *et al.*, 2007).

8 Conclusion

The aim of the present work was the development of a stochastic model of
 growth, and therefore an Individual Based Model for the distribution of
 data, that is compatible with the von Bertalanffy function and might be able
 to catch more of the features empirically observed.

The model developed in relation with the Doléans exponential shows interesting features. As other models already in the literature (Wang, 1999; Gudmundsson, 2005; Lv & Pitchford, 2007) it is able to explain the observed non monotonic behaviour of the variances. However, it is the first stochastic model producing paths that are increasing, thus, giving a realistic random model of individual growth.

Our main objective was mainly theoretical, but we think that the models developed in §4 can be of interest for practical applications such as stock assessment and forecasting. In this direction however some questions require a deeper investigation.

These are

- The determination (elicitation) of a suitable distribution for the maximal size L_{∞} .
- The determination of the appropriate subordinator.

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Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6