



HAL
open science

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

Tommaso Russo, Paolo Baldi, Antonio Parisi, Giuseppe Magnifico, Stefano Mariani, Stefano Cataudella

► To cite this version:

Tommaso Russo, Paolo Baldi, Antonio Parisi, Giuseppe Magnifico, Stefano Mariani, et al.. Lévy processes and stochastic von Bertalanffy models of growth, with application to fish population analysis. Journal of Theoretical Biology, 2009, 258 (4), pp.521. 10.1016/j.jtbi.2009.01.033 . hal-00554572

HAL Id: hal-00554572

<https://hal.science/hal-00554572v1>

Submitted on 11 Jan 2011

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Author's Accepted Manuscript

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

Tommaso Russo, Paolo Baldi, Antonio Parisi, Giuseppe Magnifico, Stefano Mariani, Stefano Cataudella

PII: S0022-5193(09)00029-0
DOI: doi:10.1016/j.jtbi.2009.01.033
Reference: YJTBI5440



www.elsevier.com/locate/jtbi

To appear in: *Journal of Theoretical Biology*

Received date: 4 August 2008
Revised date: 21 January 2009
Accepted date: 21 January 2009

Cite this article as: Tommaso Russo, Paolo Baldi, Antonio Parisi, Giuseppe Magnifico, Stefano Mariani and Stefano Cataudella, Lévy processes and stochastic von Bertalanffy models of growth, with application to fish population analysis, *Journal of Theoretical Biology* (2009), doi:[10.1016/j.jtbi.2009.01.033](https://doi.org/10.1016/j.jtbi.2009.01.033)

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting galley proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

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*

^b*Dipartimento di Matematica - Università di Roma Tor Vergata*

^c*Dipartimento di Scienze Statistiche - Università di Padova*

^d*Consiglio Nazionale delle Ricerche - CNR - Roma*

^e*School of Biology and Environmental Science - University College of Dublin*

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

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

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

11 Where L_∞ is the extremal length that is attained as time goes to infinity,
12 $-t_0$ is the time of conception, at which the size should be 0 and k is a
13 parameter that gives the speed of the process: the larger the value of k , the
14 quickest the growth. The VBGF is most commonly used as a descriptive
15 model of size-at-age data (Essington *et al.*, 2001). Nevertheless, equation
16 (1.1) describes the relationship between age and mean length of a

* Corresponding author. Tel.: +390672595974. Fax: +390672595965. *E-mail address:* Tommaso.Russo@Uniroma2.it

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,

43 1992; Wang & Thomas, 2003; Imsland *et al.*, 2002; Wang, 1999;
44 Gudmundsson, 2005).

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

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

52 Here L_t is the size at time t , $f(L_t, t)$ characterizes the deterministic intrinsic
53 growth (drift coefficient) of the individual (the same for all individuals);
54 $\alpha(L_t, t)$ gives the magnitude of the random fluctuations (diffusion coefficient)
55 and $B(t)$ is a standard Brownian motion, or Wiener process, which is
56 commonly used to model a variety of background and environmental
57 fluctuations in physical, financial and biological contexts, see
58 Karlin & Taylor (1981) e.g.

59 The stochastic component of these models is intended to account both for
60 the environment and the inter-individual variability. It should be stressed,
61 however, that (as already remarked in Gudmundsson, 2005) the solution of
62 an equation as (1.2) cannot be monotonically increasing and therefore
63 appears to be unsuitable to model the evolution of the size of an individual.
64 Stochastic models like the one of (1.2) are conversely well suited in order to
65 model quantities, as prices in financial markets, that are characterized by an

66 oscillating and therefore non monotonic behaviour. This aspect seems to be
 67 a drawback for a growth model of several animals like fish. In fact, for fish
 68 and other vertebrates, the physiological mechanism of growth in length (i.e.
 69 addition of bone material to the axial unit of the skeleton that is the
 70 vertebra) leads to a pattern in which the size of an individual is necessarily
 71 increasing in time (Weatherley & Gill, 1987). Let us point out that there
 72 exist no Gaussian process which is increasing. Therefore, modeling size
 73 variability through an individual growth process, can not give rise to a
 74 Gaussian distribution.

75 Closely related to the models (1.2) are those introduced in Gudmundsson
 76 (2005) where it is the derivative of the growth process that is the solution of
 77 a stochastic equation. It is possible in this way to obtain a stochastic process
 78 that is increasing. These models are interesting and deserve to be tried by
 79 testing against real data. Remark however that the mean size at time t of a
 80 population following such a model does not follow a VBGF.

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

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

87 This model displays a monotonic behaviour and considers the
 88 inter-individual variability of growth parameters, but does not account for

89 the randomness coming from the environment, which can be seen as a
90 limitation of the model.

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

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

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

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

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

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

124 2 Subordinators

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

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

129 This means in particular that the distribution of $Z_{t+h} - Z_t$ is independent of
 130 t for every $h \geq 0$ and that $Z_t - Z_s$ and $Z_v - Z_u$ are independent r.v.'s for
 131 $u < v \leq s < t$. Also the increments $Z_{t+h} - Z_t$ must be stationary, in the
 132 sense that their distribution depends on h only and not on t . The
 133 characterization of such processes (that are particular instances of Lévy
 134 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

$$dX_t = (L_\infty - X_{t-}) dZ_t \tag{4.10}$$

$$X_{-t_0} = 0$$

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

$$dY_t = -Y_{t-} dZ_t \tag{4.11}$$

$$Y_{-t_0} = L_\infty .$$

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

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

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

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

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

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

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

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

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

235 Remark also that some models already present in the literature are
 236 particular instances of (4.10). It is the case of the model (3.4) of
 237 Lv & Pitchford (2007) where the authors actually consider $Z_t = rt + \sigma B_t$.
 238 We point out again that the solution to (4.10) in this case does not have
 239 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

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

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

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

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

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

296 which, as already noted, is a von Bertalanffy equation with
 297 $k = \gamma + \alpha \log \frac{\lambda+1}{\lambda}$. The variance of X_t is also easily computed using (4.15):

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

298 It is also possible to compute the density of X_t , conditioned to the value of
 299 $L_\infty = l$, which is given by

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

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

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

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

306 for $0 < x < 1$ and $h(x) = 0$ elsewhere, then it turns out that \tilde{Z} is an inverse
 307 Gaussian process with parameters b and ρ . The density of
 308 $X_t = L_\infty(1 - e^{-\tilde{Z}_t - \gamma t})$ given $L_\infty = l$ is straightforward to compute and is

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

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

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

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

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

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

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

328 5 The Dataset

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

331 homogeneous collection of genetically and phenotypically characterized
332 North Sea Autumn Spawning herring (*Clupea harengus* L., 1758), from ICES
333 areas zones IVa, IVb and IVc. Herring is the dominant converter of
334 zooplankton production, using the biomass of copepods, mysids, euphausiids
335 in the pelagic environment of the northern hemisphere (Winters & Wheeler,
336 1987). Additionally, herring is a central prey item for higher trophic levels.
337 The spawning period of this species in the western North Sea is
338 September/October.

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

348 **6 Analysis of the herring dataset**

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

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

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

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

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

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

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

374 The normal and time change models have been estimated by means of
375 maximum likelihood, which appears to be the most natural method for
376 them. As already pointed out in §4, for the Doléans exponential model,
377 which is the most promising, the maximum likelihood method is
378 inapplicable, as the distribution of the maximal size L_∞ is not known. We
379 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}_∞ 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

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

430 7 Discussion

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

436 These aspects basically concern the inclusion of the different sources of
437 variability in growth rate among individuals, which directly determine the
438 size density observed at different ages, and the property of the growth
439 process of being increasing. In this work we developed two models based on
440 the use of subordinators as driving processes. Our aim was to provide a new
441 stochastic model, mainly of theoretical interest for the description of the
442 growth process for a large class of organisms. It turns out that one of them,
443 the model based on the Doléans exponential giving rise to a Gamma process,
444 is also able to produce an appreciable fit with the data. In particular it is
445 able to reproduce the non monotonic trend of the variance, that is the
446 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

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

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

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

491 **8 Conclusion**

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

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

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

506 These are

- 507 • The determination (elicitation) of a suitable distribution for the maximal
508 size L_∞ .
- 509 • The determination of the appropriate subordinator.

510 References

- 511 AA.VV (2007). *Report of Herring Assessment Working Group for the Area*
512 *south of 62° N*. ICES CM 2007/ACFM: 11.
- 513 ARINO, O., SHIN, Y. & MULLON, C. (2004). A mathematical derivation of
514 size spectra in fish populations. *C.R. Biol.* **327**, 245–254.
- 515 BENNETT, W., OSTRACH, D. & HINTON, D. (1995). Condition of larval
516 striped bass in a graught-stricken estuary: evaluating pelagic food web
517 limitation. *Ecol. Appl.* **5**, 680–692.
- 518 BEVERTON, R., HYLEN, A., ØSTVEDT, O.-J., ALVSVAAG, J. & ILES, T.

- 519 (2004). Growth, maturation, and longevity of maturation cohorts of
520 Norwegian spring-spawning herring. *ICES J.Mar.Scie.* **61**, 165–175.
- 521 BRETT, J. (1979). *Environmental factors and growth. In: Fish Physiology,*
522 *Vol. III, Bioenergetics and Growth.* New York: Academic Press Inc.
- 523 CASWELL, H. (2001). *Matrix population models: construction, analysis, and*
524 *interpretation.* Sunderland, Massachusetts, USA: Sinauer Associated.
- 525 CONOVER, D. & MUNCH, S. (2002). Sustaining fisheries yields over
526 evolutionary time scales. *Science* **297**(5578), 94–96.
- 527 CONT, R. & TANKOV, P. (2004). *Financial modelling with jump processes.*
528 Chapman & Hall/CRC Financial Mathematics Series. Chapman &
529 Hall/CRC, Boca Raton, FL.
- 530 DEANGELIS, D., ROSE, K., CROWDER, L., MARSHALL, E. & LIKA, D.
531 (1993). Fish cohort dynamics: Application of complementary modelling
532 approaches. *Am. Nat.* **142**(4), 604–622.
- 533 EDWARDS, A., PHILLIPS, R., WATKINS, N., FREEMAN, M., MURPHY,
534 E., AFANASYEV, V., BULDYREV, S., DA LUZ, M., RAPOSO, E. &
535 STANLEY, H. (2007). Revisiting Lévy flight search patterns of wandering
536 albatrosses, bumblebees and deer. *Nat.* **449**, 1044–1049.
- 537 ERNANDE, B., DIECKMANN, U. & HEINO, M. (2004). Adaptive changes in
538 harvested populations: plasticity and evolution of age and size at
539 maturation. *Proc. R. Soc. Lond.* **271**(1537), 415–423.
- 540 ESSINGTON, T., KITCHELL, J. & WALTERS, C. (2001). The von
541 Bertalanffy growth function, bioenergetics, and the consumption rates of
542 fish. *Can. J. Fish. Aquat. Sci.* **58**, 2129–2138.
- 543 FUJIWARA, M., KENDALL, B. & NISBET, R. (2004). Growth
544 autocorrelation and animal size variation. *Ecol. Lett.* **7**, 106–113.
- 545 GUDMUNDSSON, G. (2005). Stochastic growth. *Can. J. Fish. Aquat. Sci.*

546 **62**, 1746–1755.

547 HINRICHSSEN, H.-H., BUEHLER, V. & CLEMMESSEN, C. (2007). An
548 individual-based model for direct conversion of otolith into somatic growth
549 rates. *Fish. Oceanogr.* **16**(3), 207–215.

550 IMSLAND, A., JONASSEN, T., LANGSTON, A., HOARE, R., WERGELAND,
551 H., FITZGERALD, R., MULCAHY, M. & STEFANSSON, S. (2002). The
552 interrelation of growth performance and disease resistance of juvenile
553 atlantic halibut (*hippoglossus hippoglossus* l.) from different populations.
554 *Aquacul.* **204**, 167–177.

555 IMSLAND, A., NILSEN, T. & FOLKVORD, A. (1998). Stochastic simulation
556 of size variation in turbot: possible causes analysed with an individual
557 based-model. *J. Fish. Biol.* **53**, 237–258.

558 JORGENSEN, C., ENBERG, K., DUNLOP, E., ARLINGHAUS, R., BOUKAL,
559 S., BRANDER, K., ERNANDE, K., GARDMARK, A., JOHNSTON, F.,
560 MATSUMURA, S., PARDOE, H., RAAB, K., SILVA, A., VAINIKKA, A.,
561 DIECKMANN, U., HEINO, M. & RIJNSDORP, A. (2007). Managing
562 evolving fish stocks. *Science* **318**, 1247–1248.

563 KARLIN, S. & TAYLOR, H. M. (1981). *A second course in stochastic*
564 *processes*. New York: Academic Press Inc. [Harcourt Brace Jovanovich
565 Publishers].

566 KENDALL, B. & FOX, G. (2002). Variation among individuals and reduced
567 demographic stochasticity. *Cons. Biol.* **16**(1), 109–116.

568 KOOIJMAN, S. (2000). *Dinamic energy and mass budgets in biological*
569 *systems. Second edition*. Cambridge, UK: Cambridge University Press Inc.

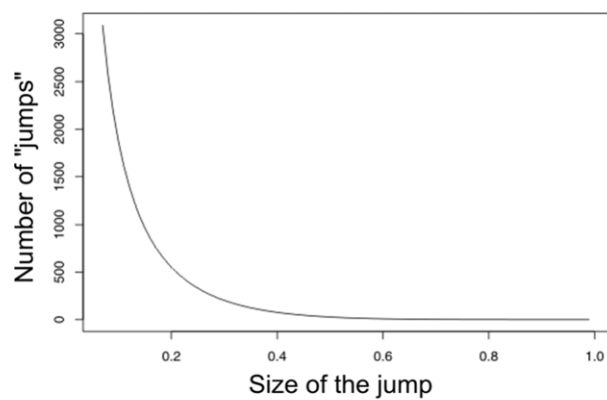
570 LV, Q. & PITCHFORD, J. W. (2007). Stochastic von Bertalanffy models,
571 with applications to fish recruitment. *J. Theoret. Biol.* **244**(4), 640–655.

572 MARIANI, S., HUTCHINSON, W., HATFIELD, D., E.M.C. RUZZANTE,

- 573 SIMMONDS, T. A. C., E.J. DAHLGREN, BRIGHAM, J., TORSTENSEN,
574 E. & CARVALHO, G. (2005). Biocomplexity in a highly migratory marine
575 pelagic fish, atlantic herring. *Mar. Ecol. Progr. Ser.* **303**, 245–257.
- 576 MULLIGAN, T. & LEAMAN, B. (1992). Length-at-age analysis: Can you get
577 what you see? *Can. J. Fish. Aquat. Sci.* **49**, 632–643.
- 578 RILLING, G. & HOUDE, E. (1999). Regional and temporal variability in the
579 distribution and abundance of bay anchovy (*Anchoa mitchilli*) eggs, larvae,
580 and adult biomass in the chesapeake bay. *Estuar.* **22**, 1096–1109.
- 581 RUZZANTE, D., MARIANI, S., BEKKEVOLD, D., ANDRE, C.,
582 MOSEGAARD, H., CLAUSEN, L., DAHLGREN, T., HUTCHINSON, W.,
583 HATFIELD, E., TORSTENSEN, E., BRIGHAM, J., SIMMONDS, E.,
584 LAIKRE, L., LARSSON, L., STET, R., RYMAN, N. & CARVALHO, G.
585 (2006). Biocomplexity in a highly migratory marine pelagic fish, atlantic
586 herring. *Proc. R. Soc. Lond.* **273**, 1459–1464.
- 587 SAINSBURY, K. (1980). Effect of individual variability on the von
588 Bertalanffy growth equation. *Can. J. Fish. Aquat. Sci.* **37**, 241–247.
- 589 SATO, K.-I. (1999). *Lévy processes and infinitely divisible distributions*,
590 vol. 68 of *Cambridge Studies in Advanced Mathematics*. Cambridge:
591 Cambridge University Press. Translated from the 1990 Japanese original,
592 Revised by the author.
- 593 SUMPTER, J. (1992). Control of growth of rainbow trout (*Oncorhynchus*
594 *mykiss*). *Aquacul.* **100**, 299–320.
- 595 UCHMANSKI, J. (2000). Individual variability and population regulation: An
596 individual-based model. *Oikos* **9**, 539–548.
- 597 VON BERTALANFFY, L. (1938). A quantitative theory of organic growth.
598 *Human Biol.* **10**, 181–213.
- 599 VON BERTALANFFY, L. (1957). Quantitative laws in metabolism and

- 600 growth. *Quart. Rev. Biol.* **32**(3), 217–231.
- 601 WANG, Y. (1999). Estimating equations for parameters in stochastic growth
602 models from tag-recapture data. *Biometrics* **55**, 900–903.
- 603 WANG, Y. & THOMAS, M. (2003). Accounting for individual variability in
604 the von Bertalanffy growth model. *Can. J. Fish. Aquat. Sci.* **52**,
605 1368–1375.
- 606 WEATHERLEY, A. & GILL, H. (1987). *The biology of fish growth*. New
607 York: Academic Press Inc. [Harcourt Brace Jovanovich Publishers].
- 608 WINTERS, G. & WHEELER, J. (1987). Clupeoid fishes of the world
609 (suborder clupeioidi). an annotated and illustrated catalogue of the
610 herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings.
611 *Can. J. Fish. Aquat. Sci.* **44**, 882–900.

Fig. 1



Accepted manuscript

Fig. 2

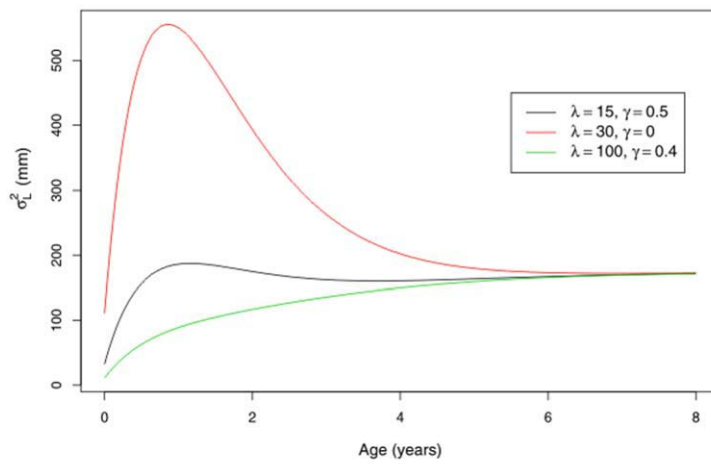
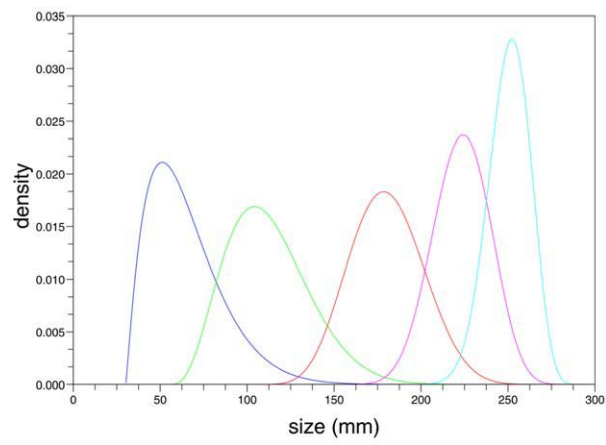
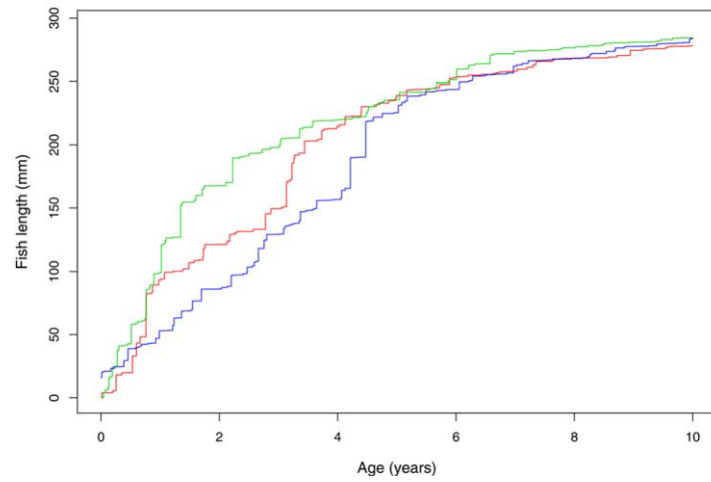


Fig. 3



Accepted manuscript

Fig. 4



Accepted manuscript

Fig. 5

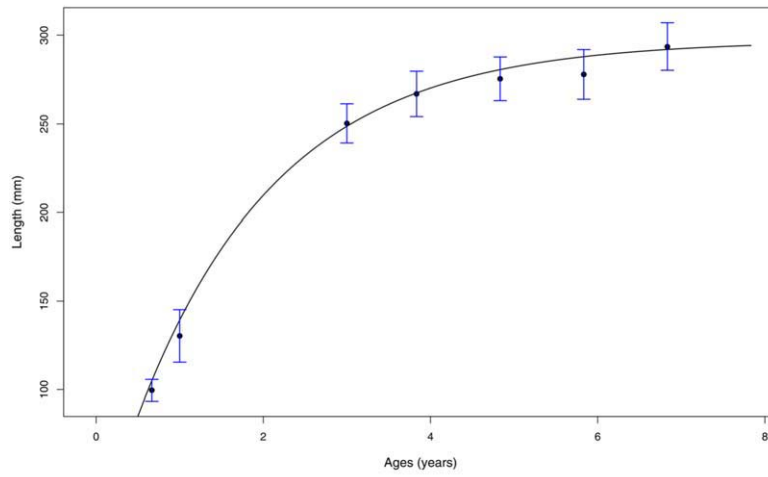


Fig. 6

