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Multitype Branching Process as Model for Phytoplankton Population and Chlorophyll-a Contained Therein

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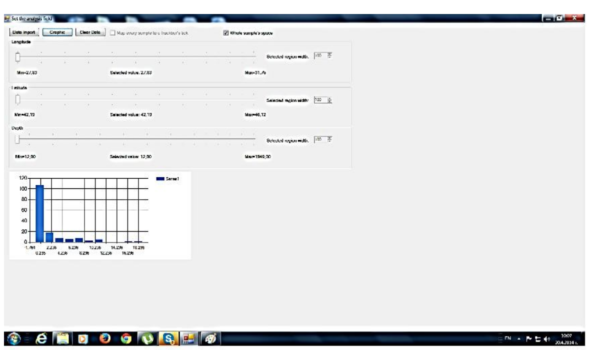
Abstract

The purpose of this research is to model a phytoplankton population localized to a particular geographical longitude, latitude and depth and try to draw conclusions about its evolution. After a random period of time τ the origination particle, phytoplankton cell, provides generation or dies. We propose model, describing the dynamics of population through multitype branching stochastic processes of Bellman-Harris. Concrete results for the expectation and asymptotic behaviour of the mean number of cells are obtained.

1. Introduction

Phytoplankton is composed of microscopic, photosynthetic species, mostly unicellular, that live in the aquatic environment. Movement in the water is mostly through transport by currents, but some phytoplankton species move using flagella. Data on the amount of chlorophyll-a may be obtained not only by the sampling, but by means of satellite. The correlation coefficient between phytoplankton and contained in it chlorophyll-a is known [1,2]. Chlorophyll-a concentrations can be a measure of phytoplankton concentrations. Therefore we can consider as a single particle in our processes, not the whole cell phytoplankton, but only the contained in the cell quantity of chlorophyll-a. The following graphics reflects the measured concentration of chlorophyll-a, according to samples taken from about 50 stations along the Bulgarian Black Sea coast during the summer of '94, '97, from 2002 to 2006, 2009 and 2011.

It gives a rough guide for the distribution of the concentration of chlorophyll-a:



The phytoplankton community grows in volume or reduces. The growth rate of phytoplankton cell depends on growth rate of the mother, but also of the size of birth.

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The growth rate depends on some random environmental factors such as the flow of sunlight, therefore for clouds, flying or swimming in the upper water layers objects that overshadow, etc. The cells which reproduce by cell division split into two daughter cells, but as a rule the two daughters are not identical. The considered phytoplankton population contains many species. For each phytoplankton species there is not just one cell, but large finite number of cells. The time to reproduction of cells is different for different types of phytoplankton, and this time differs within each species too. It depends on the environmental temperature, salinity, nutrition, light etc. The maximum rate of cell division can double up for each 10$°$C increase in temperature [8] There are seasonal change in species composition [8]. The blue-green algae Anabaena has an estimated generation time of 24 hours [3]. Phytoplankton is one of the most ancient inhabitants of our planet, playing the key role at the base of the ocean and marine food chains. In addition the phytoplankton also controls the global carbon cycle which has a significant impact on the climate regulation. Last but not least phytoplankton is a key factor in ecology.

2. Model Description

Under growth rate is meant the rate of increase in size per unit time. According to the above we assume that growth rate of the particles is a random variable. The offspring's growth rate deviation from that of the mother at the time of any division is also a random variable. Let us designated the shift by $\Delta\lambda$. From now on, let us focus only on one of the six hundred different species of phytoplankton on the Bulgarian Black Sea Coast. Let us consider the summer months for more concreteness. It is assumed the additional structure of growth rate motion on the line. We interpret the growth rate as a random variable, which move on the line. Consider a parent particle at the point x_0 , assuming a growth rate $r_0 = x_0$. After a random time it dies or splits into 2 particles , which growth rates then move to the random points $r_{01} = r_0 + x_1, r_{02} = r_0 + x_2$. We will take a normal distributed shift of the growth rate. For each cell phytoplankton there are met the next conditions [7].

Conditions 1

1. The growth rate (gr.r.) is exponential distributed and consists of two parts: a latent factor handed down by the mother, and an individual contribution.
2. The particle splits into two daughter particles of precisely equal volumes. (Fluctuations from the mean for each particle phytoplankton can be ignored)
3. The shift of growth rate is normal distributed.

The number of offspring is exactly two, both are born at the same time, but they can belong to different types. We define the random variables $\tau, \lambda, \Delta\lambda$ over the probability space (Ω, F, P). For the fixed above type of phytoplankton let us assume that gr.r. $\in Exp(\lambda)$ and the shift of the gr.r. $\Delta\lambda \in N(0,\sigma^2)$. The cells can divide or die. Here we mean death for disappearance of the cell from the population by means other than division. Bisection of cells occurs approximately when they double.

From the birth to the splitting every cell goes through several specific stages. It implements concrete activities that require a concrete time. Therefore we assume normally distributed lifetime of the cell. In addition we define the random variables $\tau_i, \lambda_i, i = 1,2,...h$ over the probability space (Ω, F, P). For practical purposes it is sufficient to determine the interval for $\Delta\lambda$ of the three sigma rule according to each type of phytoplankton. For definiteness we will consider $\Delta\lambda \in (0,3\sigma) := \Delta$. The cell is our particle and we designate it by H. The interval Δ is divided into h number of subintervals of equal length for positive, integer h. We model the multi-type age-dependent branching process W_t with h different types of particles $H_1,...,H_h$ depending on in which subinterval falls the growth rate.

The particles of H_i evolve with lifetimes $\tau_i \in N(\mu_i, \sigma_i^{*2})$, i=1,…,h, i.e. :

$$G_i(t) = P\{\tau_i \le t\} = \frac{1}{2} + \frac{1}{\sqrt{2\pi}} \int_0^t e^{-\frac{z^2}{2}} dz = \frac{1}{2} + \Phi(\frac{t-\mu_i}{\sigma})$$

p_{ij} is the probability that a daughter of H_i is a H_j. Let us be conditions that each H_j, j=1,…,h has fixed growth rate $\lambda_j := \frac{(2j-1)3\sigma}{2h}$. Thus λ_j falls right in the middle of the j-th interval Δ_j, j=1,…,h.

$Z(t) := (Z_1, Z_2, \ldots Z_h)$ is the number of particles of the different types at the moment t. On the end of the life, each particle splits, according to the probability law p_{ij} into two new particles from some of the fixed h types or dies without offspring. Namely,

(1) $$p_{ij} = \frac{1}{\sigma\sqrt{2\pi}} \int_{c_{ij}}^{c_{ij}+\frac{\sigma}{h}} e^{-\frac{t^2}{2\sigma^2}} dt$$

Where $c_{ij} := |\lambda_i - \lambda_j|$ and p_{ij} is the probability that a daughter of H_i is a H_j.

Expected generation H_j, derived from parent H_i at the moment t is $m_{ij} := E(Z_j^i(t)) < \infty$. The i-th generating function f_i will determine the distribution of the number of offspring of various types to be produced by a type i particle. The reproductive behaviour of the particles is governed by an h-dimensional generating function f(s).

(2) $$f_i(s_1, \ldots s_h) = \sum_{j_1, \ldots j_h \geq 0} p_i(j_1, \ldots j_h) s_1^{\,j} \ldots s_h^{\,j_h}$$

$0 \leq s_k \leq 1, k = 1, \ldots h,$

Where $p_i = (j_1, \ldots j_h)$ is the probability that a type i parent produces j_1 particles of type 1,…, j_h of type h.

$p(j) = (p_1(j), \ldots, p_h(j))$

$f(s) = (f_1(s), \ldots, f_h(s))$

$f(s) = \sum_{j \in R_h} p(j) s^j$, $s \in$ unit cube and R_h is the set of all points of h-dimensional Euclidean space with integer coordinates.

Let $e_i = (0, \ldots 0, 1, 0, \ldots 0)$, with the 1 in the i-th component,

(3) $$F(s,t) = \sum_j P\{Z(t) = j / Z(0) = e_i\} s^j$$

$F(s,t) = (F_1(s,t), \ldots, F_h(s,t))$

One can show that [10] :

(4) $$F_j(s,t) = s_j [1 - G_j] + \int_0^t f_i[F(s,t-y)] dG_j(y)$$

j=1,…,h

3. Expectation and Asymptotic behavior of the Mean Number of cells

3.1 Expectation

Let $m_{ij}(t) = E[Z_j(t) / Z_0 = e_i]$ and $U(t) = \|m_{ij}\|$ be the matrix of means at time t, and let M be the particle production mean matrix associated with f(s). Let for any matrix C $\|C\| := \max(|c_{ij}|, i, j = 1, \ldots, h)$. If $\|M\| < \infty$, then $\|U(t)\|$ is bounded on finite intervals, and U(t) satisfies the matrix equation [9]:

(5) $$U'(t) = D[1 - G(t)] + \int_0^t U'(t-y)M'd[G(y)]$$

Where D[x] is the diagonal matrix with x_i in the i-th place, and d[G(y)] is the diagonal matrix with dG(y) in the i-th entry.

According [9] U(t) is the unique solution bounded on finite intervals.

$A(t) := EZ(t) = E(Z_1(t),...,Z_h(t)) = (EZ_1(t),...,EZ_h(t))$

i.e. $A(t) = (A_1(t),...,A_h(t))$ for $A_i(t) = EZ_i(t)$, i=1,…,h.

By differentiating this equation it can be shown that the mean vector of the process, satisfies the linear equation

(6) $$A(t) = 1 - G(t) + m\int_0^t A(t-u)G(du)$$

The solutions of the integral equation (6) (equation of the renewal) is:

(7) $$A_i(t) = 1 - G_i(t) + m_i \int_0^t (1 - G_i(t-u))dH_i(m_i, u)$$

Where $m_i = \frac{\partial f_i}{\partial s_i}(1,...,1)$ for i=1,2,…,h and we have:

(8) $$H_i(a_i, t) = \sum_{n=1}^{\infty} m_i^{n-1}(G_i(t))^{*n}$$

and

(9) $$(G_i(t))^{*n} = \int_0^t (G_i(t-u))^{*(n-1)} dG_i(u)$$

3.2 Asymptotic behavior of the Mean Number of Cells

It is known for one-type Bellman-Harris process $Z\wedge(t)$, with $A\wedge(t) := EZ\wedge(t)$, $m\wedge := f'\wedge(1) > 1$, the relevant distribution function $G\wedge(t)$-continuous and $\alpha\wedge$ -the corresponding Malthusian parameter:

(10) $$A\wedge(t) \approx e^{\alpha t} \frac{\int_0^\infty e^{-\alpha\wedge u}(1 - G\wedge(u))du}{m\wedge \int_0^\infty u e^{-\alpha\wedge u} dG\wedge(u)} = e^{\alpha\wedge t} \frac{m\wedge - 1}{\alpha\wedge m\wedge^2 \int_0^\infty u e^{-\alpha\wedge u} dG\wedge(u)}$$

From the last equation for our multi-type Bellman-Harris process we get following,

$$A(t) \approx e^{\alpha t} \frac{m-1}{\alpha m^2 \int_0^\infty u e^{-\alpha u} dG(u)}$$,i.e.

(11) $$A(t) \approx e^{\alpha t} \frac{m-1}{\alpha m^2 \frac{1}{\sigma\sqrt{2\pi}} \int_0^\infty u e^{-\alpha u} e^{-\frac{(u-\mu)^2}{2\sigma^2}} du}$$

If we define $J := \frac{1}{\sigma\sqrt{2\pi}}\int_0^{\infty} ue^{-\alpha u}e^{-\frac{(u-\mu)^2}{2\sigma^2}}du$, after some arithmetic for $\beta := \alpha\sigma^2, i.e. \beta_i := \alpha_i\sigma_i^2, i = 1,...,N$ we derive,

$$J := \frac{e^{-\beta(2\mu-3\beta)}}{\sigma\sqrt{2\pi}}\int_0^{\infty} ue^{(u-\mu+\beta)^2}du$$

From above and for $t := u + \beta - \mu$ we get,

(12) $$J := \frac{e^{-\beta(2\mu-3\beta)}}{\sigma\sqrt{2\pi}}\int_{\beta-\mu}^{\infty}(t-(\beta-\mu))e^{-t^2}dt$$

From the last equation we get,

$$J = \frac{e^{-\beta(2\mu-3\beta)}}{\sigma\sqrt{2\pi}}\left(\frac{e^{-(\beta-\mu)^2}}{2} - (\beta-\mu)\int_{\beta-\mu}^{\infty}e^{-t^2}dt\right)$$

And finally:

(13) $$A(t) \approx e^{\alpha t}\frac{m-1}{\alpha m^2\frac{e^{-\beta(2\mu-3\beta)}}{\sigma\sqrt{2\pi}}\left(\frac{e^{-(\beta-\mu)^2}}{2} - (\beta-\mu)\int_{\beta-\mu}^{\infty}e^{-t^2}dt\right)}$$

(14) $$A_i(t) \approx e^{\alpha_i t}\frac{m_i-1}{\alpha_i m_i^2\frac{e^{-\beta_i(2\mu_i-3\beta_i)}}{\sigma_i\sqrt{2\pi}}\left(\frac{e^{-(\beta_i-\mu_i)^2}}{2} - (\beta_i-\mu_i)\int_{\beta_i-\mu_i}^{\infty}e^{-t^2}dt\right)}$$

i=1,…,h

$$\int_{\beta-\mu}^{\infty}e^{-t^2}dt = \frac{-\sqrt{\pi}}{2}(erf(\beta-\mu)-1)$$

Here $erf(\beta-\mu)$ means the error function,

$$erf(\beta-\mu) := \frac{2}{\sqrt{\pi}}\int_0^{\beta-\mu}e^{-t^2}dt$$

Let us use the designation,

$$\Phi(x) := \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{x}e^{-\frac{t^2}{2}}dt, \ \lim_{x\to\infty}\Phi(x) = 1$$

And

$$\Phi_0(x) := \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{x}e^{-\frac{t^2}{2}}dt = \Phi(x) - \frac{1}{2}$$

Under both designations above for Gaussian error-integral we have:

(15) $$erf(x) = \frac{1}{\sqrt{2\pi}}\int_0^{x}e^{-\frac{t^2}{2}}dt = 2\Phi_0(x\sqrt{2}), \ \lim_{x\to\infty}erf(x) = 1$$

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