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Modeling bounded random fluctuations in biological systems: application to the chemostat model with two species

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Abstract: The chemostat model is used in many situations to represent biological systems in which micro-organisms grow on abiotic resources. Nevertheless, most of the times, the deterministic versions of this model are analyzed in spite of random fluctuations that frequently appear in real life ecosystems. We model and analyze random fluctuations on the input flow in the chemostat model, that are bounded inside a given interval that could be provided by practitioners. We use the Ornstein-Uhlenbeck process which has already proved to be a suitable tool when modeling biological systems. In the present work, we consider the chemostat model with two competing species, for which the Competitive Exclusion Principle holds in absence of disturbances. We show that the kind of fluctuations on the input that we consider here allows the coexistence of species.

Keywords: Chemostat model, population competition, Ornstein-Uhlenbeck process, bounded fluctuations, random inputs.

1. INTRODUCTION

Bioprocesses based on micro-organisms are met in many kinds of real life applications, such as water purification, food fermentation, pharmaceutical industry... Among the three classical operating modes: batch, fed-batch, continuous, we focus in this work on the continuous one (also called chemostat), which is the one that is naturally subject to external disturbances, being an open system. The so-called *Theory of the chemostat* has received many attentions in the literature (see for instance the textbooks Smith and Waltman (1995); Harmand et al. (2017)).

Let us first recall the classical (deterministic) chemostat model with two species, given by the following system of ordinary differential equations

$$\frac{ds}{dt} = (s_{in} - s)D - \mu_1(s)x_1 - \mu_2(s)x_2, \qquad (1)$$

$$\frac{dx_1}{dt} = -Dx_1 + \mu_1(s)x_1, \qquad (2)$$

$$\frac{dx_2}{dt} = -Dx_2 + \mu_2(s)x_2, \qquad (3)$$

where $s = s(t)$, $x_1 = x_1(t)$ and $x_2 = x_2(t)$ denote the concentrations of the substrate and of both species, respectively. s_{in} is the input concentration of substrate, D

the dilution rate of the input flow and $\mu_i(\cdot)$ are the specific growth functions of the species, that we shall classically consider as Monod functions:

$$\mu_i(s) = \frac{m_i s}{a_i + s},$$

where m_i denotes the maximal specific growth rate of the species and a_i the half-saturation constant (for simplicity, we have assumed without loss of generality that the yield conversion of each species is equal to 1).

For this model, the Competitive Exclusion Principle states that apart exceptional values of D, no more than one species can survive on the long term. More precisely, defining the break-even concentrations as follows

$$\lambda_i := \sup\{s \in [0, s_{in}]; \mu_i(s) < D\},$$

the species that survive at steady state is the one that has the lowest λ_i (which has then necessarily to be below s_{in}). Although this Principle has been confirmed at lab scale (see Hansen and Hubbell (1980)), there are many real life situations for which it has not been observed. Many possible explanations have been proposed and discussed in the literature. In particular, the one that considers time-varying dilution rates $D(\cdot)$ appears to be often plausible. Nevertheless, the conditions for a time-varying input to maintain coexistence are quite strong (mostly periodic

signals have been studied in the literature). Surprisingly, random disturbances have been much less considered in the chemostat model with more than one species. Let us underline that realistic realizations of random $D(\cdot)$ have to be bounded, and that adding classically a standard Wiener is not entirely satisfactorily. In order to notice that, we refer the reader to Caraballo et al. (2016, 2019, 2017b,a) where the authors consider the simplest chemostat model and replace the deterministic dilution rate D by $D + \alpha\dot{\omega}(t)$, where $\omega(t)$ denotes the standard Wiener process in a certain probability space $(\Omega, \mathcal{F}, \mathbb{P})$ and α is the amount of noise.

To avoid the drawbacks of unbounded realizations coming from the standard Wiener process, we consider in our approach another stochastic process, the so-called Ornstein-Uhlenbeck (O-U) process, which will be introduced in Section 2. Thanks to the O-U process, we will be able to perturb the input flow in system (1)-(3), similarly to the case when considering the standard Brownian motion, i.e., we will replace D by $D + \alpha z_{\beta,\gamma}^*(\theta_t\omega)$, where $\alpha > 0$ denotes the intensity of noise and $z_{\beta,\gamma}^*(\theta_t\omega)$ is the O-U process. As it will be proved, this approach will allow us to obtain better results concerning not only the persistence of total biomass but also the coexistence of both species.

Therefore, the resulting random model is given as the following one

$$\frac{ds}{dt} = (s_{in} - s)(D + \alpha z_{\beta,\gamma}^*(\theta_t\omega)) - \mu_1(s)x_1 - \mu_2(s)x_2,$$
(4)

$$\frac{dx_1}{dt} = -(D + \alpha z_{\beta,\gamma}^*(\theta_t\omega))x_1 + \mu_1(s)x_1,$$
(5)

$$\frac{dx_2}{dt} = -(D + \alpha z_{\beta,\gamma}^*(\theta_t\omega))x_2 + \mu_2(s)x_2.$$
(6)

Thanks to the analysis of the random system (4)-(6), we will be able to provide conditions which ensure the extinction of both species and, more interesting, conditions under which the persistence of the total biomass and the coexistence of both species is also ensured in the sense that there exists $\eta > 0$ such that

$$\lim_{t \to +\infty} x_i(t) \geq \eta > 0, \quad i = 1, 2,$$
(7)

differently to other contributions providing definitions that are not as strong as ours (see, for, instance Xu et al. (2013)).

More precisely, in this work we shall assume that the graphs of the growth functions μ_i have a common intersection point on the open interval $(0, s_{in})$. In other words, none of the species has a systematic advantage on the other one. Such situations often happen in real life in terms of "compromise": one species is specialist of low values of the resource, while at the opposite the other one grows faster under large levels of the resource.

Assumption 1. There exists $s^\star \in (0, s_{in})$ such that

$$(\mu_1(s) - \mu_2(s)).(s - s^\star) > 0$$

for any $s \in [0, s_{in}] \setminus \{s^\star\}$.

One can then consider the particular value $D^\star = \mu_1(s^\star) = \mu_2(s^\star)$. For the very precise case $D(t) = D^\star$ for any t, coexistence of species is mathematically possible. In practice, it is very unlikely to maintain the dilution rate at this exact value on a large time interval. A small variation will eventually lead to the extinction of one of the species, although this can take time (see Hansen and Hubbell (1980); El Hajji and Rapaport (2009)). However, oscillating between values upper and lower than $D^\star$, alternating advantage to each species, is the core of the possibility of coexistence of species with periodic $D(\cdot)$, as been studied in the literature (see Butler et al. (1985)). One may wonder if time-varying functions $D(\cdot)$ that are exactly periodic (and that moreover satisfy a coexistence condition in terms of integral constraints to ensure the stability of the periodic solution with two species), is plausible or not in real life. In the present work, we shall consider random dilution rates $D(\cdot)$ about the nominal value $D^\star$, that appear to us more realistic.

The paper is organized as follows: in Section 2 we present the Ornstein-Uhlenbeck process since it is the tool which allows us to model the random perturbations that we consider realistic in real life. Then, in Section 3 we analyze the resulting random chemostat by providing results concerning the existence and uniqueness of global solution, existence of absorbing and attracting sets and its internal structure in order to obtain detailed information about the behavior of the system. Therefore, in Section 4 we provide numerical simulations to support the results proved in the previous sections. In Section 5 we state some final comments.

2. THE ORNSTEIN-UHLENBECK PROCESS

In this section, we present the Ornstein-Uhlenbeck process, the main tool used in this paper when modeling bounded random fluctuations, which is defined as the following random variable

$$z_{\beta,\gamma}^*(\theta_t\omega) = -\beta\gamma \int_{-\infty}^{0} e^{\beta s}\theta_t\omega(s)ds, \quad t \in \mathbb{R}, \ \omega \in \Omega, \ \beta, \gamma > 0,$$
(8)

solving the Langevin equation

$$dz + \beta z dt = \gamma d\omega.$$

We notice that ω denotes the standard Wiener process in a certain probability space $(\Omega, \mathcal{F}, \mathbb{P})$, β and γ are positive parameters and θ_t denotes the usual Wiener shift flow given by

$$\theta_t\omega(\cdot) = \omega(\cdot + t) - \omega(t), \quad t \in \mathbb{R}.$$

The O-U process given by (8) is a stationary mean-reverting Gaussian stochastic process where $\beta > 0$ is the *mean reversion constant* that reflects the strength with which the process is attracted by the mean or, in other words, how *strongly* our system reacts under some perturbation, and $\gamma > 0$ is the *volatility constant* which represents the variation or the size of the noise. In fact, the O-U process can describe the position of some particle by taking into account the friction, which is the main difference with the standard Wiener process and makes our perturbations to be a better approach to the real ones than

the ones obtained when using simply the standard Wiener process. In addition, the O-U process could be understood as a generalization of the standard Wiener process as well in the sense that it would correspond to take $\beta = 0$ and $\gamma = 1$ in (8).

Let us discuss the influence of both parameters β and γ on the evolution of the O-U process.

Fixed $\beta > 0$. Then, the volatility of the process increases for larger values of γ and the evolution of the process is smoother for smaller values of γ, which is totally reasonable since γ decides the amount of noise introduced to dz, the term which measures the variation of the process. Thus, the process will suffer much more disturbances for larger values of γ as be in Figure 1, where we simulate two realizations of the O-U process with $\beta = 1$ and we take $\gamma = 0.1$ (blue) and $\gamma = 0.5$ (orange).
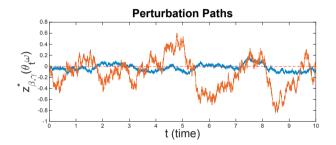

Fig. 1. Effects of the mean reversion constant

Fixed $\gamma > 0$. In this case the process tends to go further away from the mean value when considering smaller values of β and the attraction of the mean value increases for larger values of β which is totally logical since β has a huge influence on the drift of the Langevin equation (8), as can observed in Figure 2, where we simulate two realizations of the O-U process with $\gamma = 0.1$ and we take $\beta = 1$ (blue) and $\beta = 10$ (orange).
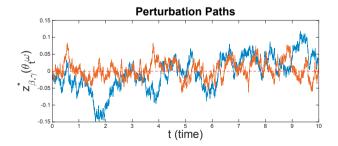

Fig. 2. Effects of the volatility constant

Now we provide some important properties which will be crucial for the analysis in this paper.

Proposition 1. There exists a θ_t-invariant set $\widetilde{\Omega} \in \mathcal{F}$ of Ω of full $\mathbb{P}$−measure such that for $\omega \in \widetilde{\Omega}$ and $\beta, \gamma > 0$, we have

(i) the random variable $|z_{\beta,\gamma}^*(\omega)|$ is tempered:

$$\lim_{t \to \infty} e^{-\delta t} \sup_{t \in \mathbb{R}} |z_{\beta,\gamma}^*(\theta_{-t}\omega)| = 0, \quad \text{for all } \delta > 0,$$

for a.e. $\omega \in \widetilde{\Omega}$.

(ii) the mapping

$$(t, \omega) \to z_{\beta,\gamma}^*(\theta_t\omega) = -\beta\gamma \int_{-\infty}^{0} e^{\beta s}\omega(t+s)\mathrm{d}s + \omega(t)$$

is a stationary solution of (8) with continuous trajectories;

(iii) for any $\omega \in \widetilde{\Omega}$ one has

$$\lim_{t \to \pm\infty} \frac{|z_{\beta,\gamma}^*(\theta_t\omega)|}{t} = 0;$$

$$\lim_{t \to \pm\infty} \frac{1}{t} \int_0^t z_{\beta,\gamma}^*(\theta_s\omega)ds = 0;$$

$$\lim_{t \to \pm\infty} \frac{1}{t} \int_0^t |z_{\beta,\gamma}^*(\theta_s\omega)|ds = \mathbb{E}[z_{\beta,\gamma}^*] < \infty;$$

(iv) finally, for any $\omega \in \widetilde{\Omega}$,

$$\lim_{\beta \to \infty} z_{\beta,\gamma}^*(\theta_t\omega) = 0, \quad \text{for all } t \in \mathbb{R}.$$

For the proof of the previous proposition we refer the readers to Al-Azzawi et al. (2017) (Lemma 4.1) and Arnold (1998); Caraballo et al. (2004).

3. RANDOM CHEMOSTAT MODEL

We come back to the random model (4)-(6) with two species. Our aim in this section is to provide first a result concerning the existence and uniqueness of global solution and then to derive some properties concerning the existence of absorbing and attracting set for the dynamics of that system. Finally, we will give results concerning the internal structure of the attracting set of system since it will allow us to obtain more detail information about the long-time behavior of the random chemostat model (4)-(6).

Firstly, let us consider a strictly positive interval $[D_l, D_u] \subset \mathbb{R}$, which is typically chosen by practitioners. Thanks to Proposition 1 (iv), for every fixed event $\omega \in \Omega$, there exists $\beta > 0$ large enough such that $D + \alpha z_{\beta,\gamma}^*(\theta_t\omega) \in [D_l, D_u]$ for every time. In such a case β depends actually on the event ω and the corresponding random system (4)-(6) may not generate a random dynamical system. Nevertheless, this is not a problem at all since we can analyze the dynamics of system (4)-(6) for every fixed event ω. As a result, we will be able to prove all the results forwards in time instead of using the more complicated pullback convergence that we need when using the theory of random dynamical systems.

From now on, we denote the positive orthant

$$\mathcal{X} := \{(x, y, z) \in \mathbb{R}^3 \ : \ x, y, z \geq 0\}.$$

Theorem 2. System (4)-(6) possesses a unique solution $u(\cdot, 0, \omega, u_0) := (s, x_1, x_2)(\cdot, 0, \omega, u_0) \in \mathcal{C}^1([0, +\infty), \mathcal{X})$ which remains inside the positive orthant for any initial value $u_0 = (s_0, x_{10}, x_{20}) \in \mathcal{X}$.

The proof can be made by means of the classical techniques of ordinary differential equations and taking into

account that the Ornstein-Uhlenbeck process $z_{\beta,\gamma}^*(\theta_t\omega)$ is continuous for every time. We omit the proof here.

Theorem 3. The set
$$\mathcal{B}_0 := \{(x,y,z) \in \mathcal{X} \ : \ x+y+z=s_{in}\} \qquad (9)$$
is a deterministic attracting set for system (4)-(6) in forward sense, i.e.,
$$\lim_{t\to+\infty} \sup_{u_0 \in F} \inf_{b_0 \in B_0} |u(t;0,\omega,u_0) - b_0| = 0,$$
where F denotes a bounded set in the phase plane $\mathbb{R}^2$ and u_0 denotes the initial value of the solution of system (4)-(6).

Proof. For any $\varepsilon > 0$, consider the set
$$\mathcal{B}_\varepsilon := \{(x,y,z) \in \mathcal{X} \ : \ s_{in} - \varepsilon \le x+y+z \le s_{in}+\varepsilon\}$$
Define the variable $q = s + x_1 + x_2$ which satisfies the following random differential equation
$$\frac{dq}{dt} = -(D + \alpha z_{\beta,\gamma}^*(\theta_t\omega))q,$$
whose solution is given by
$$q(t;0,\omega,q(0)) = q(0)e^{-Dt-\alpha\int_0^t z_{\beta,\gamma}^*}.$$
By taking limit when t goes to infinity in (3), we have
$$\lim_{t\to+\infty} q(t;0,\omega,q(0)) = 0, \qquad (10)$$
then we deduce that for any $\varepsilon > 0$, $\mathcal{B}_\varepsilon$ is a deterministic absorbing set for system (4)-(6).

Now, we are interested in studying the internal structure of the attracting set (9) since it will give much more detailed information concerning the long-time dynamics of the chemostat. The following result provides a condition under which both species in the random chemostat model (4)-(6) becomes extinct.

Proposition 4. Each species i such that $\mu_i(s_{in}) < D$ goes to extinction for any realization of the noise.

Proof. Let $\varepsilon = D - \mu_i(s_{in})$. As $q(t;0,\omega,q(0))$ tends to s_{in} for any ω when t goes to infinity, we deduce that there exists a finite time $T(\varepsilon,\omega)$ such that $\mu_i(s_{in}) < D - \varepsilon/2$ for any $t > T(\varepsilon,\omega)$ and then, from the equation for the species,
$$\frac{dx_i}{dt} < -(D + \alpha z_{\beta,\gamma}^*(\theta_t\omega)x_i + \left(D - \frac{\varepsilon}{2}\right)x_i,$$
for $i = 1, \ 2$, whose solution is given by
$$x_i(t;0,\omega,x_i(0)) < x_i(0)e^{-\frac{\varepsilon}{2}t - \alpha\int_0^t z_{\beta,\gamma}^*(\theta_s\omega)ds}.$$

Thus, the attracting set (9) reduces to a point $(s_{in},0,0)$ which means the extinction of the species.

The next result provides conditions which ensure the persistence of both species in the chemostat model (4)-(6) in the *strong* sense (7).

Theorem 5. Persistence of the total biomass of the species can be ensured provided
$$s_{in} > \underline{m}, \quad \underline{m}s_{in} > D_u(\bar{a} + s_{in}), \qquad (11)$$

where $\underline{m} = \min_i m_i$ and $\bar{a} = \max a_i$. In addition, we recall that D_u is the largest value that the realizations of the perturbed input flow $D + \alpha z_{\beta,\gamma}^*(\theta_t\omega)$ could take for every time.

Proof. From (10), $-\varepsilon \le x_1 + x_2 + s + s_{in} \le \varepsilon$ for all $\varepsilon > 0$. Now, we define the total biomass of species $x = x_1 + x_2$ whence $s \le \varepsilon + s_{in} - x$ and $s \ge -\varepsilon + s_{in} - x$.

Thus, by differentiation, the total biomass of species satisfies
$$\frac{dx}{dt} = -(D + \alpha z_{\beta,\gamma}^*(\theta_t\omega))x + \frac{m_1 s}{a_1 + s}x_1 + \frac{m_2 s}{a_2 + s}x_2$$
$$> -D_u x + \frac{\underline{m}}{\bar{a}+s}x_1 + \frac{\underline{m}}{\bar{a}+s}x_2$$
$$\ge -D_u x + \frac{\underline{m}(-\varepsilon+s_{in}-x)}{\bar{a}+\varepsilon+s_{in}-x}x.$$

Hence, by evaluating the previous inequalities for $x = x^*$, where
$$x^* = \frac{\underline{m}s_{in} - \bar{a}D_u - s_{in}D_u}{\underline{m} - D_u},$$
it follows
$$\left.\frac{dx}{dt}\right|_{x=x^*} > \left[-D_u + \frac{\underline{m}s_{in} - \underline{m}x^*}{\bar{a}+s_{in}-x^*}\right]x^*$$
$$= 0,$$
for some ε small enough, as long as (11) is verified.

Now, since $-\varepsilon \le x_1 + x_2 + s + s_{in} \le \varepsilon$ for all $\varepsilon > 0$, we have $x \le \varepsilon + s_{in} - s$. Then, from the equation for the substrate we have
$$\frac{ds}{dt} = (D + \alpha z_{\beta,\gamma}^*(\theta_t\omega))(s_{in} - s) - \frac{m_1 s}{a_1 + s}x_1 - \frac{m_2 s}{a_2 + s}x_2$$
$$> D_l(s_{in} - s) - \frac{\bar{m}s}{\underline{a}+s}x_1 - \frac{\bar{m}s}{\underline{a}+s}x_2$$
$$\ge D_l(s_{in} - s) - \frac{\bar{m}s}{\underline{a}+s}(s - \varepsilon - s_{in}),$$
with $\bar{m} = \max_i m_i$ and $\underline{a} = \min_i a_i$.

Thus, by evaluating the previous inequalities for $s = s^*$, where
$$s^* = \frac{D_l\underline{a}}{\bar{m} - D_l},$$
it follows
$$\left.\frac{ds}{dt}\right|_{s=s^*} > (s_{in} - s^*)\left(D - \frac{\bar{m}s^*}{\underline{a}+s^*}\right)$$
$$= 0$$
for some ε small enough, since $s^* > 0$ and, from (11), we have $\bar{m}s_{in} > D_l(\underline{a} + s_{in})$ thus $s^* < s_{in}$.

Then, we have that the attracting set (9) of the random system (4)-(6), reduces to

$\mathcal{A} = \{(x, y, z) \in \mathcal{X} : x + y + z = s_{in}, x^* \leq y + z, x > s^*\}.$

From the previous result, we can deduce the persistence of the total biomass in the *strong* sense (7) under some conditions which are totally logical from the point of biology.

In this section we provided conditions under which each species become extinct and also some conditions which allow us to prove that the total microbial biomass persists.

The simulations conducted in next Section 4 show that coexistence of both species is indeed verified when considering random bounded fluctuations of the input flow affected by the O-U process when $D = D^\star$, which leads us to posit the conjecture.

Conjecture 1. Under Assumption 1, random bounded fluctuations of the input flow affected by the O-U process $D^\star + \alpha z^*_{\beta,\gamma}(\theta_t \omega)$ ensures coexistence of species.

4. NUMERICAL SIMULATIONS

In this section we provide some numerical simulations which support the theoretical results presented in the previous sections.

We have chosen the following values for the parameters of the growth functions: $a_1 = 2$, $m_1 = 3$, $a_2 = 1$, $m_2 = 2$. One can check that Assumption 1 is satisfied with $D^\star = \frac{m_2 - m - 1}{a_2 - a_1} = 1$.

From now on, the blue dashed lines represent the solution of the deterministic system, i.e., without fluctuations, and the rest are different realizations of the solution of the random one. In addition, we consider the initial value $(s_0, x_{10}, x_{20}) = (5, 5, 2.5)$ in every case and we take $\gamma = 0.2$ as the volatility constant and $s_{in} = 7$.

In every figure three panels are displayed showing the dynamics of the substrate and the two species individually respect to the time.

In Figure 3, the intensity of the noise is $\alpha = 4$, the mean reversion constant is $\beta = 20$ and the input flow $D = 2$.
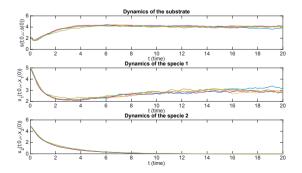

Fig. 3. Extinction of the second species. $\alpha = 4$, $\beta = 20$ and $D = 2$

As a result, we can observe that the second species become extinct while the first ones persist. This is not surprising by taking into account Proposition 4 since $\mu_1(s_{in}) = 2.34 > 2 = D$ and $\mu_2(s_{in}) = 1.75$ which would mean the extinction of the first ones.

In Figure 4 we increase the value of input flow $D = 2.5$ and we take $\beta = 2$ as the mean reversion constant. The rest of the parameters do not change respect to the ones used in the previous figure.
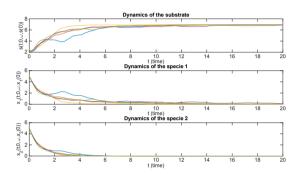

Fig. 4. Extinction of both species. $\alpha = 4$, $\beta = 2$ and $D = 2.5$

In this case we can observe that $\mu_1(s_{in}) = 2.34 > 2.5 = D$ $\mu_2 = 1.75 > 2.5 = D$ whence, as proved in Proposition 4, we obtain the extinction of both species.

In Figure 5, the intensity of the noise is $\alpha = 4$, the mean reversion constant is $\beta = 10$ and the input flow $D = 1$.
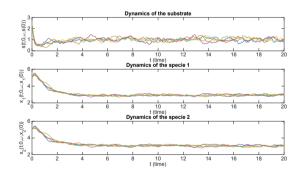

Fig. 5. Coexistence of both species. $\alpha = 4$, $\beta = 10$ and $D = 1$

In this case we can observe that both species persist. We would like to remark that conditions (11) in Theorem 5 are fulfilled then we can ensure that the total microbial biomass persist. We are precisely in the case of Conjecture 1, since $D = D^\star$.

Eventually, in Figure 6 we increase the intensity of the noise to $\alpha = 1$, the mean reversion constant $\beta = 14$ and we do not change the values of the parameters respect to the ones in the previous case.
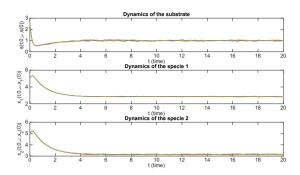
Fig. 6. Coexistence of both species. $s_{in} = 7$, $a_1 = 2$, $m_1 = 3$, $a_2 = 1$, $m_2 = 2$, $\alpha = 1$, $\beta = 14$ and $D = 1$

As in the previous case, conditions (11) in Theorem 5 are verified then the total microbial biomass persist. In addition, as explained in Conjecture 1, we have coexistence of both species. Respect to the previous case, we remark that fluctuations in this case are not so large and the realizations of the solution of every state variable is closer to the deterministic value which is not strange since we decreased the intensity of the noise and increased the mean reversion constant respect to the previous case.

5. FINAL COMMENTS

In this paper, the O-U process proves again to be a very good tool when modeling process in real life which are known to be random but bounded. Thanks to its properties, it is possible to model such a randomness as it happens in reality from practitioners and, apart from that, it allows us to ensure the persistence of the total biomass and, what is the most interesting point for biologists, it seems to be possible to provide conditions under which both species in the experiment persist, as it can be seen in the numerical simulations.

As a result, the O-U process does not only provide us a very useful toll in modeling but also a very suitable process which allows us to conclude interesting results from the point of view of the applications by means of easy but not trivial computations.

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