MODELING AND ANALYSIS OF RANDOM AND STOCHASTIC INPUT FLOWS IN THE CHEMOSTAT MODEL

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Abstract. In this paper we study a new way to model noisy input flows in the chemostat model, based on the Ornstein-Uhlenbeck process. We introduce a parameter β as drift in the Langevin equation, that allows to bridge a gap between a pure Wiener process, which is a common way to model random disturbances, and no noise at all. The value of the parameter β is related to the amplitude of the deviations observed on the realizations. We show that this modeling approach is well suited to represent noise on an input variable that has to take non-negative values for almost any time.

1. Introduction. Chemostat refers to a laboratory device used for growing microorganisms in a cultured environment and has been regarded as an idealization of nature to study microbial ecosystems at steady state, which is a really important and interesting problem since they can be used to study genetically altered microorganisms, waste water treatment (see e.g. [16, 25]) and play an important role in theoretical ecology (see e.g. [3, 15, 23, 24, 26]). The simplest chemostat device consists of three interconnected tanks called feed bottle, culture vessel and collection vessel. The nutrient is pumped from the first tank to the culture vessel, where the interactions between the species and the nutrients take place, and there is also another flow being pumped from the culture vessel to the third one such that the volume of the culture vessel remains constant. Derivation and analysis of chemostat models are well documented in [19, 21] and references therein.

Some standard assumptions for simple chemostat models are usually imposed, for instance, it is common to suppose that the availability of the nutrient and its

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supply rate are fixed. However, they are very strong restrictions since the real world is non-autonomous and stochastic. This is one of the reasons which encourage us to go further away from deterministic systems and study stochastic chemostat models.

Let us consider the classical chemostat model

\[
\begin{align*}
\frac{ds}{dt} &= (s_{in} - s) \frac{Q}{V} - \mu(s)x, \\
\frac{dx}{dt} &= -\frac{Q}{V} x + \mu(s)x,
\end{align*}
\] (1.1)

where \(s(t)\) and \(x(t)\) denote concentrations of the nutrient and the microbial biomass, respectively; \(s_{in}\) denotes the input concentration, \(Q\) is the input flow, \(V\) is the volume of liquid media inside the culture vessel and the ratio \(Q/V\), which is also denoted by \(D\), is called dilution rate. We notice that all parameters are supposed to be positive and a function Holling type-II, \(\mu(s) = ms/(a + s)\), is used as functional response of the microorganisms describing how the nutrient is consumed by the species, where \(a\) is the half-saturation constant and \(m\) denotes the maximal specific growth rate of microorganisms. Sometimes we will refer to this function as the consumption function or growth function as well.

There exist many different ways of modeling stochasticity and/or randomness in some deterministic model, see e.g. [4, 5, 6, 18, 22, 28, 29, 30, 32, 33]. Considerations of stochastic processes in the chemostat model have already been tackled in the literature, but mainly on the growth function (see, for instance, [7]). This appears particularly relevant when the number of individual bacteria could be small, with a risk of extinction of the biomass population in finite time. Nevertheless, sudden extinctions in continuous cultures that are well supervised about a nominal regime are quite rare in practice. On another hand, fluctuations on the input flow that brings permanently resources to the bacterial population in continuous cultures are much likely to be observed. In the present work, we focus on the way to model these random fluctuations, taking into consideration that the effective flow rate has to stay non-negative. From the biological point of view, the fact of introducing a noisy term in the input flow of our chemostat model is a really interesting problem found in the laboratory since, for instance, it reflects the presence of particles of dirt inside the pumps or temporary clogs at the input or output of the chemostat. Then, it is well known that continuous flow is often subjected to random fluctuations with time.

In this paper we shall follow two different approaches to perturb the input flow in the chemostat model. As the volume \(V\) is constant, it is equivalent to have disturbances on the dilution rate \(D = Q/V\) instead of considering them on the input flow. On the one hand, we will consider a perturbation by making use of the well-known standard Wiener process such that we replace \(D\) by the stochastic term \(D + \omega(t)\) in the deterministic system (1.1)-(1.2), where \(\omega\) denotes the standard Wiener process and \(\alpha > 0\) represents the intensity of the noise. Thus, the corresponding stochastic system is given by

\[
\begin{align*}
\frac{ds}{dt} &= \left( s_{in} - s \right) D - \frac{msx}{a + s} dt + \alpha(s_{in} - s) d\omega(t), \\
\frac{dx}{dt} &= -\frac{Q}{V} x + \mu(s)x \\
&- \alpha x d\omega(t).
\end{align*}
\]
As will be discussed in Section 3, this common approach will lead into some drawbacks, for instance, the persistence of the microorganisms can never be ensured and some state variables can take negative values. Therefore, this stochastic process does not seem to be the best way to represent disturbances on the input flow in the chemostat model, due to the fact that it provides unrealistic situations from the biological point of view since it would mean that the pumps are reverting flow, which is not reasonable at all.

On the other hand, we will consider a suitable Ornstein-Uhlenbeck (O-U) process to perturb the dilution rate. Particularly, we are interested in replacing \( D \) by the random term \( D + \alpha z^\mu_{\beta,\nu}(\theta t_\omega) \), where \( z^\mu_{\beta,\nu}(\theta t_\omega) \) denotes some suitable O-U process which will be carefully introduced later and \( \alpha > 0 \) represents again the intensity of noise. In such a way, the resulting random model is given by the following system of random differential equations

\[
\frac{ds}{dt} = (s_{in} - s) \left[ D + \alpha z^\mu_{\beta,\nu}(\theta t_\omega) \right] - \mu(s)x, \tag{1.3}
\]

\[
\frac{dx}{dt} = - \left[ D + \alpha z^\mu_{\beta,\nu}(\theta t_\omega) \right] x + \mu(s)x. \tag{1.4}
\]

Concerning the O-U process, some essential properties will be provided which will allow us to set up a new framework and, moreover, to make calculations in the next section. To sum up some of the main ingredients to be used, for every fixed event \( \omega \), it will be possible to choose \( \beta_\omega \in \mathbb{R} \) such that the corresponding realizations of the perturbed input flow, \( D + \alpha z^\mu_{\beta,\nu}(\theta t_\omega) \), will remain for every \( t \in \mathbb{R} \) inside some strictly positive band which should be previously fixed, for instance, by practitioners. In such a way, for every fixed event \( \omega \), the resulting random chemostat model will be given by

\[
\frac{ds}{dt} = (s_{in} - s) \left[ D + \alpha z^\mu_{\beta,\nu}(\theta t_\omega) \right] - \mu(s)x, \tag{1.5}
\]

\[
\frac{dx}{dt} = - \left[ D + \alpha z^\mu_{\beta,\nu}(\theta t_\omega) \right] x + \mu(s)x. \tag{1.6}
\]

As a consequence, since \( \beta_\omega \in \mathbb{R} \) depends on the event \( \omega \) previously fixed, the solutions of system (1.5)-(1.6) may not generate a random dynamical system. Nevertheless, this does not represent any inconvenience for the analysis of the long time behavior of the random differential system (1.5)-(1.6), since it can be investigated for every fixed event \( \omega \). In fact, we will be able to obtain some results on forwards convergence (in time) of solutions, instead of the pullback convergence obtained within the framework of random dynamical systems.

This new approach, which arises from the nature of the particular noise (the suitable O-U process), leads into another unusual technique which seems to be really interesting since, for instance, it allows us to guarantee the existence of compact and attracting sets (forwards in time) which are strictly inside the positive cone, whence we will ensure the persistence of the species in the sense that there exists a number \( \eta > 0 \) such that for any non null initial biomass \( x(0) \) each realization satisfies

\[
\liminf_{t \to +\infty} x(t) \geq \eta > 0. \tag{1.7}
\]

\(^1\)We will refer to this sense throughout the whole paper when using the term “persistence”. In case of referring to another sense, we will specify the new definition.
Needless to say that this is the principal goal pursued by biologists for modeling bounded disturbances in a biological framework, differently to other several previous works as [22] where the authors consider disturbances in the chemostat model by means of the standard Wiener process and prove some results concerning the persistence of the biomass in the sense \( \liminf_{t \to +\infty} x(t) > 0 \), which is weaker than (1.7).

We also achieve some improvements comparing our results throughout this paper with the ones by Xu et al in [31] since, even though they consider stochastic noise on the dilution rate in the chemostat model, they need a condition on the parameter of the amplitude of the noise to ensure the persistence (see, for instance, Theorem 1.2 and Section 4 in [31] where the authors ensure the necessity of a smallness condition on the amount of noise \( \alpha > 0 \) whereas, in our case, modeling the disturbances with the Ornstein-Uhlenbeck process, there is no discussion needed on the amplitude of the noise to ensure the persistence (which is, in addition, in the stronger sense (1.7)). Moreover, the authors in [31] prove the results in probability while we will prove all the results almost surely, i.e., for every realization in a set of events of full measure.

The previous reasons constitute a few representative examples which support that this way of perturbing the dilution rate by using the Ornstein-Uhlenbeck process fits much better the real situations we wish to model. Apart from the advantages described above, we will also obtain some improvements with respect to the results obtained when analyzing the deterministic chemostat model (1.1)-(1.2), as we will explain in more detail in Section 2. To be more precise, in the deterministic setting the washout equilibrium \((s, 0)\) is attractive if \( D = \mu(s_{in}) \) (see [19]) whereas, in our case by using the O-U process, it is possible to prove that there exists an attracting (forwards in time) set for the solutions of our system which has several points (in fact, all of them except the washout) inside the positive cone.

The paper is organized as follows. In Sections 2 and 3 we will analyze the chemostat models perturbed by the Ornstein-Uhlenbeck process and the white noise, respectively. We will prove the existence and uniqueness of a global solution and we will also state some results regarding the existence of a compact absorbing set as well as an attracting one. Finally, in Section 4 some numerical simulations which will support the results previously proved will be also presented. In addition, we present briefly some basic concepts and results concerning the theory of random dynamical systems (RDSs) in Appendix.

2. The chemostat model with random input flow. In this section, we are interested in investigating system (1.3)-(1.4), where a random perturbation on the dilution rate has been introduced by means of a suitable O-U process, as explained in the introductory section. To this end, we will present a new framework which will be a bit different from the ones used in previous papers by Caraballo and several coauthors (see e.g. [7, 8, 9, 11]), where the theory of random dynamical systems is used.

2.1. The Ornstein-Uhlenbeck process. Let \( W \) be a two sided Wiener process. Kolmogorov’s theorem ensures that \( W \) has a continuous version, that we will denote by \( \omega \), whose canonical interpretation is as follows: let \( \Omega \) be defined by

\[
\Omega = \{ \omega \in \mathcal{C}(\mathbb{R}, \mathbb{R}) : \omega(0) = 0 \},
\]
\( F \) the Borel \( \sigma \)-algebra on \( \Omega \) generated by the compact open topology (see [2] for details) and \( \mathbb{P} \) the corresponding Wiener measure on \( F \). We consider the Wiener shift flow given by

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

Then, \((\Omega, F, \mathbb{P}, \{\theta_t\}_{t \in \mathbb{R}})\) is a metric dynamical system (see Appendix for details).

Now, let us introduce the following Ornstein-Uhlenbeck (O-U) process defined on \((\Omega, F, \mathbb{P}, \{\theta_t\}_{t \in \mathbb{R}})\) as the random variable given by

\[
z_{\beta, \nu}^{\ast}(\theta_t \omega) = -\beta \nu \int_{-\infty}^{0} e^{\beta s} \theta_t \omega(s) \, ds, \quad t \in \mathbb{R}, \; \omega \in \Omega, \; \beta, \nu > 0, \tag{2.1}
\]

which solves the following Langevin equation (see [2, 12, 13])

\[
d z + \beta z \, dt = \nu d\omega(t), \quad t \in \mathbb{R}. \tag{2.2}
\]

The O-U process given by (2.1) is a stationary mean-reverting Gaussian stochastic process where \( \beta > 0 \) is a mean reversion constant that represents the strength with which the process is attracted by the mean or, in other words, how strongly our system reacts under some perturbation, and \( \nu > 0 \) is a volatility constant which represents the variation or the size of the noise independently of the amount of the noise \( \alpha > 0 \). 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 model to be a better approach to the real ones, specially when modeling processes in microbiology as in our case. In addition, the O-U process can be understood as a kind of generalization of the standard Wiener process, which would correspond to take \( \beta = 0 \) and \( \nu = 1 \) in (2.1).

By taking into account the definition of both parameters \( \beta \) and \( \nu \) involved in the Langevin equation (2.2), we highlight the following relevant observations concerning the effect caused by each of them on the evolution of the process.

2.1.1. **Fixed \( \beta > 0 \).** Then, the volatility of the process is larger if we consider a larger \( \nu \). However, the evolution of the process is smoother when we take a smaller value of \( \nu \). This is reasonable since \( \nu \) decides the amount of noise introduced to \( dz \), which measures the variation of the process, hence the process will be subjected to suffer many more changes when choosing a larger value of \( \nu \). We can observe this behavior in Figure 1 where we simulate two realizations of the perturbed dilution rate \( D + \alpha z_{\beta, \nu}^{\ast}(\theta_t \omega) \) with \( D = 2, \alpha = 0.8, \beta = 2 \) and we consider \( \nu = 0.1 \) (blue) and \( \nu = 0.5 \) (orange).

2.1.2. **Fixed \( \nu > 0 \).** Then, the process tends to go further away from the mean value if we consider a smaller value of \( \beta \). However, the attraction of the mean increases when taking a larger \( \beta \), which is quite logical since \( \beta \) has a huge influence on the drift of the Langevin equation (2.2). For instance, we can observe this behavior in Figure 2, where we simulate two realizations of the perturbed dilution rate \( D + \alpha z_{\beta, \nu}^{\ast}(\theta_t \omega) \) with \( D = 2, \alpha = 0.8, \nu = 0.5 \) and we take \( \beta = 2 \) (blue) and \( \beta = 10 \) (orange).

Now, we establish the following result involving important ergodic properties held by the O-U process which will be used at several places in the sequel.

**Proposition 2.1.** There exists a \( \theta_t \)-invariant set \( \bar{\Omega} \in F \) of \( \Omega \) of full \( \mathbb{P} \)-measure such that for \( \omega \in \bar{\Omega} \) and \( \beta, \nu > 0 \), we have

1. the random variable \( |z_{\beta, \nu}^{\ast}(\omega)| \) is tempered (see Definition 4.3).
Figure 1. Realizations of the perturbed dilution rate with $D = 2$, $\alpha = 0.8$ and $\beta = 2$

Figure 2. Realizations of the perturbed dilution rate with $D = 2$, $\alpha = 0.8$ and $\nu = 0.5$

(ii) the mapping

$$(t, \omega) \rightarrow z_{\beta, \nu}^*(\theta_t \omega) = -\beta \nu \int_{-\infty}^{0} e^{\beta s} \omega(t + s) ds + \omega(t)$$

is a stationary solution of (2.2) with continuous trajectories;

(iii) for any $\omega \in \Omega$ one has:

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

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

$$\lim_{t \to \pm \infty} \frac{1}{t} \int_{0}^{t} |z_{\beta, \nu}^*(\theta_s \omega)| ds = \mathbb{E}[z_{\beta, \nu}^*] < \infty;$$

(iv) finally, for any $\omega \in \tilde{\Omega}$, $\lim_{\beta \to \infty} z_{\beta, \nu}^*(\theta_t \omega) = 0$, for all $t \in \mathbb{R}$.

Remark 2.1. We note that the proof of (iv) can be found in [1] (see Lemma 4.1) and we refer the readers to [2, 12] for the proof of (i)-(iii).
Then, if we restrict the metric dynamical system to $\tilde{\Omega}$, we obtain a new metric dynamical system, see [10]. For simplicity, we will denote this new metric dynamical system by the old symbols, namely $(\Omega, F, \mathcal{F}, \{\theta_t\}_{t \in \mathbb{R}})$.

Our aim in this section is to analyze the long-time behavior of system (1.3)-(1.4). To this end, let us first fix a strictly positive interval, namely $(\bar{b}, \hat{b}) \subset \mathbb{R}$, where $\bar{b} > \hat{b} > 0$. Thanks to the last item in Proposition 2.1, for each $\omega \in \Omega$, it is possible to choose $\beta \in \mathbb{R}$ large enough such that the corresponding realization of the perturbed input flow, $D + \alpha z_{\beta, \nu}^s(\theta_t \omega)$, remains inside the interval $(\bar{b}, \hat{b})$ for every $t \in \mathbb{R}$. Nevertheless, it is not possible to ensure, from a theoretical point of view, that there exists some $\beta \in \mathbb{R}$ such that almost all realizations of the perturbed input flow remains in $(\bar{b}, \hat{b})$. Because of this reason, we will analyze our system (1.3)-(1.4) for every fixed $\omega \in \Omega$. As stated above, we know that it is possible to find $\beta_{\omega} \in \mathbb{R}$ such that $D + \alpha z_{\beta, \nu}^s(\theta_t \omega) \in (\bar{b}, \hat{b})$ for every $t \in \mathbb{R}$, then we need to analyze the following random system

$$\frac{ds}{dt} = (s_{in} - s) \left[ D + \alpha z_{\beta, \nu}^s(\theta_t \omega) \right] - \mu(s)x,$$

$$\frac{dx}{dt} = - \left[ D + \alpha z_{\beta, \nu}^s(\theta_t \omega) \right] x + \mu(s)x.$$

We would like to remark that the choice of $\beta$ depends on $\omega \in \Omega$, this is the reason to write $\beta_{\omega}$ in the previous system. Then, $\beta_{\omega}$ acts in practice as a control parameter. However, once an event $\omega \in \Omega$ is fixed, we have that $\beta_{\omega}$ is also a fixed real number, thus we will rewrite $\beta_{\omega} = \beta$ and we will focus on analyzing the system (1.3)-(1.4) for every fixed $\omega \in \Omega$. The interesting fact is that the attracting sets for the solutions will not depend on $\omega$ even though $\beta$ depends on $\omega$, so we will obtain a non random set where all solutions for all realizations will approach to.

In the rest of the section, we will prove the existence and uniqueness of a global solution of system (1.3)-(1.4) as well as the existence of a strictly positive forward attracting set for its solutions, whence we will ensure that the microorganism concentration will converge asymptotically to a strictly positive interval or, in other words, we will be able to guarantee the persistence of the species.

Before starting with the analysis previously motivated, let us recall the classical Monod expression

$$\mu(s) = \frac{ms}{a + s}, \quad \text{for all } s \geq 0,$$

denoting the consumption for the specific growth rate function of the species. Then, we define the following constants

$$\bar{s} := \mu^{-1}(\bar{b}) \quad \text{and} \quad \hat{s} := \mu^{-1}(\hat{b}) \quad (2.3)$$

which will be essential henceforth. See Figure 3 where we plot the mapping $s \rightarrow \mu(s)$ and overlap a realization of the perturbed input flow as well without taking into account the dependency of time.

2.2. The random chemostat model. We are interested in analyzing the following random chemostat model

$$\frac{ds}{dt} = - \left[ D + \alpha z_{\beta, \nu}^s(\theta_t \omega) \right] s - \mu(s)x + s_{in} \left[ D + \alpha z_{\beta, \nu}^s(\theta_t \omega) \right], \quad (2.4)$$

$$\frac{dx}{dt} = - \left[ D + \alpha z_{\beta, \nu}^s(\theta_t \omega) \right] x + \mu(s)x, \quad (2.5)$$
where \( \mu(s) = ms/(a + s) \) denotes the Holling type-II consumption function as the functional response of the microorganisms. Henceforth, \( \omega \in \Omega \) is fixed and \( \beta \in \mathbb{R} \) is also a parameter which has been fixed such that \( D + \alpha z^*_{\beta, \nu}(\theta_\omega) \in (\underline{b}, \bar{b}) \) for all \( t \in \mathbb{R} \).

In this section, \( \mathcal{X} = \{(x, y) \in \mathbb{R}^2 : x \geq 0, y \geq 0\} \) denotes the positive cone.

**Theorem 2.1.** For any initial pair \( v_0 := (s_0, x_0) \in \mathcal{X} \), system \((2.4)-(2.5)\) possesses a unique global solution

\[
v(t; 0, \omega, v_0) := (s(t; 0, \omega, v_0), x(t; 0, \omega, v_0)) \in C^1([0, +\infty), \mathcal{X})
\]

with \( v(0; 0, \omega, v_0) = v_0 \), where \( s_0 := s(0; 0, \omega, v_0) \) and \( x_0 := x(0; 0, \omega, v_0) \).

**Proof.** We set \( v(t; 0, \omega, v_0) := (s(t; 0, \omega, v_0), x(t; 0, \omega, v_0)) \) such that system \((2.4)-(2.5)\) can be rewritten as

\[
\frac{dv}{dt} = L(\theta_\omega) \cdot v + F(v, \theta_\omega),
\]

where

\[
L(\theta_\omega) = \begin{pmatrix} -(D + \alpha z^*_{\beta, \nu}(\theta_\omega)) & -m \\ 0 & -(D + \alpha z^*_{\beta, \nu}(\theta_\omega)) + m \end{pmatrix}
\]

and \( F : \mathcal{X} \times [0, +\infty) \longrightarrow \mathbb{R}^2 \) is given by

\[
F(\xi, \theta_\omega) = \begin{pmatrix} \frac{ma}{a + \xi_1} \xi_2 + s_{in}D + \alpha s_{in} z^*_{\beta, \nu}(\theta_\omega) \\ \frac{-ma}{a + \xi_1} \xi_2 \end{pmatrix},
\]

where \( \xi = (\xi_1, \xi_2) \in \mathcal{X} \).

Since \( z^*_{\beta, \nu}(\theta_\omega) \) is continuous, \( L \) generates an evolution system on \( \mathbb{R}^2 \). Moreover, we notice that \( F(\cdot, \theta_\omega) \in C^1(\mathcal{X} \times [0, +\infty); \mathbb{R}^2) \) which implies that it is locally Lipschitz with respect to \( (\xi_1, \xi_2) \in \mathcal{X} \). Therefore, system \((2.4)-(2.5)\) possesses a unique local solution. Now, we prove that the unique local solution of system \((2.4)-(2.5)\) is defined for any forward time and is, in fact, a unique global one. To this end, we define the new state variable \( q(t) := s(t) + x(t) - s_{in} \). Then, \( q \) satisfies the following differential equation

\[
\frac{dq}{dt} = -\left[ D + \alpha z^*_{\beta, \nu}(\theta_\omega) \right] q,
\]
whose solution is given by

\[ q(t; 0, \omega, q(0)) = q(0)e^{-Dt - \alpha \int_0^t z^*_\theta,\omega(\theta, \omega)ds}. \] (2.7)

It is straightforward to check that \( q \) does not blow up at any finite time, thanks to the positiveness of the dilution rate and the ergodic properties of the O-U process (see Proposition 2.1, (iii)), moreover \( q \) is bounded. In addition, after solving (2.5) we have the following upper bound for the \( x \)-equation

\[ x(t; 0, \omega, x(0)) \leq x(0)e^{-(D-m)t - \alpha \int_0^t z^*_\theta,\omega(\theta, \omega)ds}, \]

since \( \mu(t) \leq m \) for any \( s \geq 0 \).

In conclusion, \( x \) is also bounded by an expression which does not blow up at any finite time. Therefore, \( s \) does not blow up either and we can conclude that our chemostat model (2.4)-(2.5) possesses a unique global solution.

Moreover, since \( x \equiv 0 \) solves (2.5) and every realization of our noise remains in some strictly positive interval, we conclude that

\[ \frac{ds}{dt} \bigg|_{s=0} = [D + \alpha z^*_\theta,\omega(\theta, \omega)]s_{\text{in}} > 0. \]

Thus, we can ensure the unique solution of system (2.4)-(2.5) to be in the positive cone \( \mathcal{X} \) for every initial value \( v_0 \in \mathcal{X} \).

Now, we are interested in proving the existence of an attracting set. From now on, \( F \subset \mathcal{X} \) denotes a bounded set in the positive cone.

**Theorem 2.2.** For any \( \varepsilon > 0 \), there exists a deterministic compact absorbing set \( B_\varepsilon \subset \mathcal{X} \) for the solution of our system (2.4)-(2.5), i.e., there exists \( T_F(\omega, \varepsilon) > 0 \) such that for every given initial pair \( v_0 \in F \), the solution corresponding to \( v_0 \) remains inside \( B_\varepsilon \) for all \( t \geq T_F(\omega, \varepsilon) \).

**Proof.** Consider again \( q(t) = s(t) + x(t) - s_{\text{in}} \). Then, thanks to (2.7), we obtain

\[ \lim_{t \to +\infty} q(t; 0, \omega, q(0)) = 0. \] (2.8)

Thus, given \( v_0 \in F \) and any \( \varepsilon > 0 \), there exists \( T_F(\omega, \varepsilon) > 0 \) such that

\[ -\varepsilon \leq q(t; 0, \omega, q(0)) \leq \varepsilon \]

for every \( t \geq T_F(\omega, \varepsilon) \).

Then,

\[ B_\varepsilon := \{(s, x) \in \mathcal{X} : s_{\text{in}} - \varepsilon \leq s + x \leq s_{\text{in}} + \varepsilon\}. \] (2.9)

is a compact absorbing set in \( \mathcal{X} \). \hfill \square

Therefore, thanks to Theorem 2.2, we have that

\[ B_0 := \{(s, x) \in \mathcal{X} : s + x = s_{\text{in}}\} \]

is a deterministic attracting set for the solution of our system (2.4)-(2.5) in forward sense, i.e.,

\[ \lim_{t \to +\infty} \sup_{v_0 \in F} \inf_{b_0 \in B_0} |v(t; 0, \omega, v_0) - b_0|_{\mathcal{X}} = 0. \]

In the sequel, we will analyze the internal structure of the previous attracting set of our chemostat model (2.4)-(2.5) by developing a deeper analysis of both equations of the nutrient and microorganism concentrations separately, and taking also into account the asymptotic behavior of the total mass \( s + x \).
Proposition 2.2. Assume that the following condition
\[ D > \mu(s_{in}) \] (2.10)
holds. Then, the corresponding attracting set of the chemostat model (2.4)-(2.5) is reduced to a singleton component which is given by \{(s_{in},0)\}.

Proof. We know that \(B_\varepsilon\), which is given by (2.9), provides us a compact absorbing set for the solutions of our system for every \(\varepsilon > 0\). Then, for any \(\varepsilon > 0\), there exists \(T_F(\omega, \varepsilon) > 0\) such that for every given initial pair \(v_0 \in F\), \(s(t) \leq s_{in} + \varepsilon\) for all \(t \geq T_F(\omega, \varepsilon)\), whence we can deduce that \(\mu(s(t)) \leq \mu(s_{in} + \varepsilon)\) since \(\mu(\cdot)\) is an increasing function. Therefore, from (2.5) we obtain
\[ \frac{dx}{dt} \leq -[D + \alpha z_\beta^*(\theta, \omega)] x + \mu(s_{in} + \varepsilon) x, \]
whose solution satisfies
\[ x(t; 0, \omega, x_0) \leq x_0 e^{-(D - \mu(s_{in} + \varepsilon))t - \alpha \int_0^t z_\beta^*(\theta, \omega) ds}. \]

In addition, by assuming that condition (2.10) holds true, we know that there exists \(\varepsilon_0 > 0\) such that \(D > \mu(s_{in} + \varepsilon)\) for every \(\varepsilon \in (0, \varepsilon_0)\). Thus, we can easily deduce that \(x\) tends to zero when \(t\) goes to infinity as long as (2.10) is satisfied.

Therefore, the attracting set for the solution of the chemostat model (2.4)-(2.5) consists of a singleton component which is given by \{(s_{in},0)\}. \qed

Remark 2.2. We would like to highlight that Proposition 2.2 can be easily proved by assuming \(D > m\). Nevertheless, assumption (2.10) is sharper than \(D > m\) even though it requires a bit more of technicalities.

The next result proves that it is possible to ensure the persistence of the microorganisms under some condition involving the parameters of the model.

Theorem 2.3. Assume that
\[ \bar{s} < s_{in} \] (2.11)
holds true, where \(\bar{s}\) is defined as in (2.3). Then, for any \(\varepsilon > 0\), there exists a compact absorbing set \(\hat{B}_\varepsilon \subset \mathcal{X}\), which is strictly contained in the positive cone \(\mathcal{X}\), for the solutions of our chemostat model (2.4)-(2.5).

Proof. We recall that \(q(t) = s(t) + x(t) - s_{in}\) satisfies the differential equation (2.6). Hence, from (2.8) we have that, for any \(\varepsilon > 0\), there exists \(T_F(\omega, \varepsilon) > 0\) such that for every given initial pair \(v_0 \in F\), we obtain
\[ -\varepsilon \leq q(t; 0, \omega, q(0)) \leq \varepsilon \] (2.12)
for every \(t \geq T_F(\omega, \varepsilon)\).

Now, we analyze the differential equation for the substrate independently of the dynamics of system (2.4)-(2.5) since it will help us to guarantee the existence of a compact absorbing set for the substrate equation, which will be totally contained in the positive cone \(\mathcal{X}\). Then, from (2.4), as \(q(t) = s(t) + x(t) - s_{in}\), we have the
following differential equation satisfied by the substrate
\[
\frac{ds(t; 0, \omega, s_0)}{dt} = (s_{in} - s(t; 0, \omega, s_0))(D + \alpha z_{\beta, \nu}^*(\theta t \omega)) - \mu(s(t; 0, \omega, s_0))x(t; 0, \omega, x_0)
\]
\[
= (s_{in} - s(t; 0, \omega, s_0))(D + \alpha z_{\beta, \nu}^*(\theta t \omega)) - \mu(s(t; 0, \omega, s_0))q(t; 0, \omega, q_0)
\]
\[
- \mu(s(t; 0, \omega, s_0))(s_{in} - s(t; 0, \omega, s_0)).
\] (2.13)

Hence, from (2.12) we can obtain the following bounds for the \(s\)-equation
\[
\frac{ds(t; 0, \omega, s_0)}{dt} \leq (s_{in} - s(t; 0, \omega, s_0))(D + \alpha z_{\beta, \nu}^*(\theta t \omega)) - \mu(s(t; 0, \omega, s_0))(s_{in} - s(t; 0, \omega, s_0)) + \varepsilon m
\]
and
\[
\frac{ds(t; 0, \omega, s_0)}{dt} \geq (s_{in} - s(t; 0, \omega, s_0))(D + \alpha z_{\beta, \nu}^*(\theta t \omega)) - \mu(s(t; 0, \omega, s_0))(s_{in} - s(t; 0, \omega, s_0)) - \varepsilon m,
\]
for every \(v_0 \in F, \varepsilon > 0\) and for all \(t \geq T_F(\omega, \varepsilon)\) (where we recall that \(\mu\) satisfies \(\mu(s) < m\) for any \(s > 0\)).

We study now both differential inequalities when \(s = \underline{s}\) and \(s = \bar{s}\), respectively, where \(\underline{s}\) and \(\bar{s}\) are defined as in (2.3). On the one hand, thanks to (2.11), we have
\[
\frac{ds(t; 0, \omega, s_0)}{dt} \bigg|_{s = \bar{s}} \leq (s_{in} - \bar{s})(D + \alpha z_{\beta, \nu}^*(\theta t \omega)) - \mu(\bar{s})(s_{in} - \bar{s}) + \varepsilon m
\]
\[
\leq (s_{in} - \bar{s})\pi_\varepsilon + \varepsilon m,
\]
for every \(v_0 \in F, \varepsilon > 0\) and for all \(t \geq T_F(\omega, \varepsilon)\), where \(\pi_\varepsilon := \sup_{t \geq 0} \pi_- (t)\) and \(\pi_- (t) = (D + \alpha z_{\beta, \nu}^*(\theta t \omega)) - \mu(\bar{s})\).

In this case, as long as we take \(\varepsilon \in (0, -(s_{in} - \bar{s})\pi_\varepsilon / m)\), we have \((s_{in} - \bar{s})\pi_\varepsilon + \varepsilon m < 0\), and
\[
\frac{ds(t; 0, \omega, s_0)}{dt} \bigg|_{s = \bar{s}} < 0. \tag{2.14}
\]

On the other hand, from (2.11) we deduce that \(s_{in} > \underline{s}\). Then, we similarly have
\[
\frac{ds(t; 0, \omega, s_0)}{dt} \bigg|_{s = \underline{s}} \geq (s_{in} - \underline{s})(D + \alpha z_{\beta, \nu}^*(\theta t \omega)) - \mu(\underline{s})(s_{in} - \underline{s}) - \varepsilon m
\]
\[
\geq (s_{in} - \underline{s})\pi^\varepsilon - \varepsilon m,
\]
for every \(v_0 \in F, \varepsilon > 0\) and for all \(t \geq T_F(\omega, \varepsilon)\), where \(\pi^\varepsilon := \inf_{t \geq 0} \pi^+ (t)\) and \(\pi^+ (t) = (D + \alpha z_{\beta, \nu}^*(\theta t \omega)) - \mu(\underline{s})\).

Now, it is enough to consider \(\varepsilon \in (0, (s_{in} - \underline{s})\pi^\varepsilon / m)\) in order to have \((s_{in} - \underline{s})\pi^\varepsilon - \varepsilon m > 0\). Thus,
\[
\frac{ds(t; 0, \omega, s_0)}{dt} \bigg|_{s = \underline{s}} > 0. \tag{2.15}
\]

From (2.14) and (2.15) we obtain a frame for the \(s\) variable:
\[
\underline{s} < s(t; 0, \omega, s_0) < \bar{s}
\]
for every given $\varepsilon \in (0, \min\{(s_{\infty} - \bar{s})\pi^+/m, -(s_{\infty} - \bar{s})\pi_-/m\})$ and for all $t \geq T_F(\omega, \varepsilon)$, which means that the interval $(\bar{s}, \bar{s})$ is an absorbing set for equation (2.4) in forward sense.

In the sequel, we will be able to guarantee the persistence of the microorganisms by proving that there also exists another absorbing set, associated to the equation describing the dynamics of the microbial biomass, which will be also totally contained in the positive cone $X$.

As a consequence of the previous reasoning, we obtain the following inequalities

$$-\bar{s} + s_{\infty} - \varepsilon < x(t; 0, \omega, x_0) < -\bar{s} + s_{\infty} + \varepsilon,$$

for every given $\varepsilon \in (0, \min\{(s_{\infty} - \bar{s})\pi^+/m, -(s_{\infty} - \bar{s})\pi_-/m\})$ and for all $t \geq T_E(\omega, \varepsilon)$.

Thanks to the previous study, we deduce that the strictly positive interval $(s_{\infty} - \bar{s}, s_{\infty} - \bar{s})$ is an absorbing set for (2.5), the equation which describes the dynamics of the microorganisms.

As a result,

$$\hat{B}_\varepsilon = \{(s, x) \in X : s + x = s_{\infty} + \varepsilon, \bar{s} \leq s \leq \bar{s}, s_{\infty} - \bar{s} - \varepsilon \leq x \leq s_{\infty} - \bar{s} + \varepsilon\} \quad (2.16)$$

defines a compact absorbing set for our chemostat model (2.4)-(2.5) in forward sense.

Thanks to the previous result, we obtain that

$$\hat{B}_0 = \{(s, x) \in X : s_{\infty} \leq s + x \leq s_{\infty}, \bar{s} \leq s \leq \bar{s}, s_{\infty} - \bar{s} \leq x \leq s_{\infty} - \bar{s}\} \quad (2.17)$$

is a strictly positive attracting set for the solution of our system (2.4)-(2.5) in forward sense (see Figure 4).

![Figure 4. Attracting set $\hat{B}_0$](image)

We notice that, as long as condition (2.11) holds true, we obtain a new attracting set $\hat{B}_0$ which is clearly smaller than the initial one $B_0$. Thus, we can ensure the persistence of the microbial biomass.

From Proposition 2.2, Theorem 2.3 and taking into account the arguments used in the corresponding proofs, it is possible to analyze all the cases involving both conditions (2.10) and (2.11) which are presented in Table 1 as a summary concerning the internal structure of the attracting set $\hat{B}_0$ and explained in more details below.
In order to provide a complete description of the asymptotic behavior of the chemostat model with random input flow, we explain Table 1 in more detail. Firstly, it is easy to check that some cases are not compatible. In addition, thanks to Proposition 2.2 and Theorem 2.3, we know that the biomass becomes extinct as long as (2.10) holds true and we deduce persistence if (2.11) is fulfilled. However, there are more cases which can be analyzed. On the one hand, if \( D = \mu(s_{in}) \) and \( s_{in} = \bar{s} \) hold true, we can check that it is possible to redo the proof of Theorem 2.3 but, in this case, (2.14) becomes an equality implying that the attracting set, \( \hat{B}_0 \), is given by

\[
\hat{B}_0 = \{(s, x) \in X : s + x = s_{in}, \underline{s} \leq s \leq s_{in}, 0 \leq x \leq s_{in} - \underline{s}\}. \tag{2.18}
\]

On the other hand, as long as \( s_{in} < \bar{s} \) and \( D \leq \mu(s_{in}) \) are fulfilled, we can also redo the proof of Theorem 2.3 but, in this case, we cannot obtain (2.14). Thus, the attracting set, \( \hat{B}_0 \), also verifies (2.18).

From the previous analysis, it is worth mentioning that, in a different form to the deterministic case, where the washout equilibrium \((s_{in}, 0)\) is attractive if \( D = \mu(s_{in}) \) holds true (whence we obtain the extinction of the microbial biomass), see e.g. [19, 27], it is possible to deduce a relevant improvement when considering random disturbances on the input flow as in this section since, although it is not possible to guarantee the persistence of the microorganisms in the strong sense (1.7), we are able to ensure that the corresponding attracting set has several points (in fact, all of them except the washout) inside the positive cone.

### 3. The chemostat model with stochastic input flow

In this section, we will follow previous works (see e.g. [7, 9]) and analyze the chemostat model (1.1)-(1.2) where the dilution rate is perturbed by the standard Wiener process or white noise. We will perform a change of variables involving an O-U process such that the transformed random ordinary differential system generates a random dynamical system. Thanks to this fact, we will obtain a non-autonomous deterministic system for every fixed \( \omega \in \Omega \) (random system) which is much more tractable from the mathematical point of view than the original stochastic one. After that, we will
prove that there exists a unique global solution of the resulting random system and we will also provide some results concerning the existence, uniqueness and analysis of the internal structure of the pullback random attractor. Finally, we will recover the pullback random attractor associated to the original stochastic chemostat model.

We firstly replace the dilution rate $D$ by the perturbed one $D + \alpha \omega(t)$, such that we obtain the following stochastic chemostat model understood in Ito’s sense

\begin{align*}
    ds & = \left[(s_{in} - s)D - \frac{m sx}{a + s}\right] dt + \alpha(s_{in} - s) d\omega(t), \quad (3.1) \\
    dx & = \left[-Dx + \frac{m sx}{a + s}\right] dt - \alpha x d\omega(t), \quad (3.2)
\end{align*}

where $\omega \in \Omega$ denotes the canonical version of the standard Brownian motion and $\alpha \geq 0$ represents the intensity of noise.

Now, we can rewrite (3.1)-(3.2) as the following stochastic differential system

\begin{align*}
    ds & = \left[(s_{in} - s)\bar{D} - \frac{m sx}{a + s}\right] dt + \alpha(s_{in} - s) \circ d\omega(t), \\
    dx & = \left[-\bar{D}x + \frac{m sx}{a + s}\right] dt - \alpha x \circ d\omega(t),
\end{align*}

understood in Stratonovich’s sense, where

\[ \bar{D} := D + \frac{\alpha^2}{2}. \]

First of all, let us define two new variables $\sigma = \sigma(\cdot)$ and $\kappa = \kappa(\cdot)$ as follows

\[ \sigma(t) = (s(t) - s_{in})e^{\alpha z^*(\theta, \omega)} \quad \text{and} \quad \kappa(t) = x(t)e^{\alpha z^*(\theta, \omega)}, \]

where $z^*$ denotes now the O-U process $z^*_{\theta, \omega}$ defined as in (2.1). We also recall that $(\Omega, \mathcal{F}, \mathbb{P}, \{\theta_t\}_{t \in \mathbb{R}})$ denotes the metric dynamical system given after Proposition 2.1.

Now, by differentiation, we obtain the following random differential system

\begin{align*}
    \frac{d\sigma}{dt} & = -\bar{D} \alpha z^* \sigma - \frac{m(s_{in} + \sigma e^{-\alpha z^*(\theta, \omega)})}{a + s_{in} + \sigma e^{-\alpha z^*(\theta, \omega)} \kappa}, \quad (3.3) \\
    \frac{d\kappa}{dt} & = -\bar{D} \alpha z^* \kappa + \frac{m(s_{in} + \sigma e^{-\alpha z^*(\theta, \omega)})}{a + s_{in} + \sigma e^{-\alpha z^*(\theta, \omega)} \kappa}. \quad (3.4)
\end{align*}

Throughout this section, we will denote $\tilde{X} := \{(x, y) \in \mathbb{R}^2 : x \in \mathbb{R}, y \geq 0\}$, the upper-half plane.

**Theorem 3.1.** For any $\omega \in \Omega$ and any initial value $u_0 := (\sigma_0, \kappa_0) \in \tilde{X}$, system (3.3)-(3.4) possesses a unique global solution

\[ u(\cdot; 0, \omega, u_0) := (\sigma(\cdot; 0, \omega, u_0), \kappa(\cdot; 0, \omega, u_0)) \in \mathcal{C}^1([0, +\infty), \tilde{X}) \]

with $u(0; 0, \omega, u_0) = u_0$, where $\sigma_0 := \sigma(0; 0, \omega, \sigma_0)$ and $\kappa_0 := \kappa(0; 0, \omega, \kappa_0)$. Moreover, the solution mapping generates an RDS $\varphi_u : \mathbb{R}^+ \times \Omega \times \tilde{X} \to \tilde{X}$ defined as

\[ \varphi_u(t, \omega)u_0 := u(t; 0, \omega, u_0), \quad \text{for all} \ t \in \mathbb{R}^+, u_0 \in \tilde{X}, \ \omega \in \Omega, \]

in other words, the value at time $t$ of the solution of system (3.3)-(3.4) with initial state $u_0$ at time zero.
Proof. System (3.3)-(3.4) can be rewritten as
\[
\frac{du}{dt} = L(\theta_t) \cdot u + F(u, \theta_t),
\]
where
\[
L(\theta_t) = \begin{pmatrix}
-(\bar{D} + \alpha z^*) & -m \\
0 & -(\bar{D} + \alpha z^*) + m
\end{pmatrix}
\]
and \( F : \tilde{X} \times [0, +\infty) \to \mathbb{R}^2 \) is given by
\[
F(\xi, \theta_t) = \begin{pmatrix}
ma \\
ma + s_{in} + \xi_1 e^{-\alpha z^*(\theta_t)}
\end{pmatrix},
\]
where \( a = (\xi_1, \xi_2) \in \tilde{X} \).

Then, there exists a unique local solution of system (3.3)-(3.4) thanks to classical results from the theory of ordinary differential equations.

Now, we will prove that the unique local solution is in fact a unique global one (i.e., that is defined for any \( t \geq 0 \)). By defining \( \tilde{q}(t) := \sigma(t) + \kappa(t) \) it is easy to check that \( \tilde{q} \) satisfies the differential equation
\[
\frac{d\tilde{q}}{dt} = -(\bar{D} + \alpha z^*)\tilde{q},
\]
whose solution is given by the following expression
\[
\tilde{q}(t; 0, \omega, \tilde{q}(0)) = \tilde{q}(0)e^{-\bar{D}t - \alpha \int_0^t z^*(\theta, \omega)ds}.
\]

The right side of (3.5) always tends to zero when \( t \) goes to infinity since \( \bar{D} \) is positive, thus \( \tilde{q} \) is clearly bounded. Moreover, since
\[
\left. \frac{d\sigma}{dt} \right|_{\sigma=0} = -\frac{ms_{in}}{a + s_{in}} \kappa < 0
\]
we deduce that, if there exists some \( t^* > 0 \) such that \( \sigma(t^*) = 0 \), we will have \( \sigma(t) < 0 \) for all \( t > t^* \). Owing to the previous reasoning, we will split our analysis into two different cases.

Case 1. \( \sigma(t) > 0 \) for all \( t \geq 0 \). In this case, from (3.3) we obtain
\[
\frac{d\sigma}{dt} \leq -(\bar{D} + \alpha z^*)\sigma
\]
whose solutions should satisfy
\[
\sigma(t; 0, \omega, \sigma(0)) \leq \sigma(0)e^{-\bar{D}t - \alpha \int_0^t z^*(\theta, \omega)ds}.
\]

Since \( \bar{D} \) is positive, we deduce that \( \sigma \) tends to zero when \( t \) goes to infinity, hence \( \sigma \) is bounded.

Case 2. There exists \( t^* > 0 \) such that \( \sigma(t^*) = 0 \). In this case, we already know that \( \sigma(t) < 0 \) for all \( t > t^* \) and we claim that the following bound for \( \sigma \) holds true
\[
\sigma(t; 0, \omega, \sigma(0)) > -(a + s_{in})e^{\alpha z^*(\theta, \omega)}.
\]

To prove (3.6), we suppose that there exists \( \tilde{t} > t^* > 0 \) such that
\[
a + s_{in} + \sigma(\tilde{t})e^{-\alpha z^*(\theta, \omega)} = 0,
\]
then we can find some $\varepsilon(\omega) > 0$ small enough such that $\sigma(t)$ is strictly decreasing and
\[
-(\tilde{D} + \alpha z^*(\theta t)) - \frac{m(s_{in} + \sigma(t)e^{-\alpha z^*(\theta t)})}{\alpha + s_{in} + \sigma(t)e^{-\alpha z^*(\theta t)}}\kappa(t) > 0
\]
holds for all $t \in [\tilde{t} - \varepsilon(\omega), \tilde{t}]$. Hence, from (3.7) we have
\[
\frac{d\sigma}{dt}(\tilde{t} - \varepsilon(\omega)) > 0.
\]
Consequently, there exists some $\delta(\omega) > 0$, small enough, such that $\sigma(t)$ is strictly increasing for all $t \in [\tilde{t} - \varepsilon(\omega), \tilde{t} - \varepsilon(\omega) + \delta(\omega))$, which clearly contradicts the uniqueness of solution. Hence, (3.6) holds true for all $t \in \mathbb{R}$ and we can also ensure that $\sigma$ is bounded.

Since $\sigma + \kappa$ and $\sigma$ are bounded in both cases, $\kappa$ is also bounded. Hence, the unique local solution of system (3.3)-(3.4) is a unique global one. Moreover, the unique global solution of system (3.3)-(3.4) remains in $\tilde{X}$ for every initial value in $\tilde{X}$ since $\kappa \equiv 0$ solves the same system.

Finally, the mapping $\varphi_u : \mathbb{R}^+ \times \Omega \times \tilde{X} \to \tilde{X}$ given by
\[
\varphi_u(t, \omega)u_0 := u(t; 0, \omega, u_0), \quad \text{for all } t \geq 0, \ u_0 \in \tilde{X}, \ \omega \in \Omega,
\]
defines an RDS generated by the solution of (3.3)-(3.4). The proof of this statement follows similarly to the one of Theorem 2.1, hence we omit it.

**Theorem 3.2.** There exists a tempered compact random absorbing set $B_0(\omega) \in \mathcal{E}(\tilde{X})$ for the RDS $\{\varphi_u(t, \omega)\}_{t \geq 0, \omega \in \Omega}$.

**Proof.** Thanks to (3.5), we have
\[
\tilde{q}(t; 0, \theta_{-t}\omega, \tilde{q}(0)) = \tilde{q}(0)e^{-\tilde{D}t} \int_{0}^{t} z^*(\theta s\omega)ds \xrightarrow{t \to \infty} 0.
\]

Then, for all $\varepsilon > 0$ and $u_0 \in E(\theta_{-t}\omega)$, there exists $T_E(\omega) > 0$ such that, for all $t \geq T_E(\omega)$,
\[
-\varepsilon \leq \tilde{q}(t; 0, \theta_{-t}\omega, \tilde{q}(0)) \leq \varepsilon.
\]

If we assume that $\sigma(t) \geq 0$ for all $t \geq 0$, which corresponds to Case 1 in the proof of Theorem 3.1, since $\kappa(t) \geq 0$ for all $t \geq 0$, we have that
\[
B^1_\varepsilon(\omega) := \{(\sigma, \kappa) \in \tilde{X} : \sigma \geq 0, \ \sigma + \kappa \leq \varepsilon\}
\]
is a tempered compact random absorbing set in $\tilde{X}$.

In the other case, i.e., if there exists some $t^* > 0$ such that $\sigma(t^*) = 0$, which corresponds to Case 2 in the proof of Theorem 3.1, we proved that
\[
\sigma(t; 0, \theta_{-t}\omega, \sigma(0)) > -(a + s_{in})e^{\alpha z^*(\omega)}.
\]

Hence, we obtain that
\[
B^2_\varepsilon(\omega) := \{(\sigma, \kappa) \in \tilde{X} : -\varepsilon - (a + s_{in})e^{\alpha z^*(\omega)} \leq \sigma \leq 0, \ -\varepsilon \leq \sigma + \kappa \leq \varepsilon\}
\]
is a tempered compact random absorbing set in $\tilde{X}$.

In conclusion, defining
\[
B_\varepsilon(\omega) = B^1_\varepsilon(\omega) \cup B^2_\varepsilon(\omega)
\]
\[
= \{(\sigma, \kappa) \in \tilde{X} : -\varepsilon \leq \sigma + \kappa \leq \varepsilon, \ \sigma \geq -(a + s_{in})e^{\alpha z^*(\omega)} - \varepsilon\},
\]
(see Figure 5) we obtain that $B_\varepsilon(\omega)$ is a tempered compact random absorbing set in $\tilde{X}$ for every $\varepsilon > 0$. 

Then, we have that
\[ B_0(\omega) := \{ (\sigma, \kappa) \in \bar{X} : \sigma + \kappa = 0, \sigma \geq -(a + s_{in})e^{\alpha z^*(\omega)} \} \]

is a tempered compact random absorbing set as we wanted to prove (see Figure 6).

Therefore, thanks to Proposition 4.1, it follows directly that system (3.3)-(3.4) possesses a unique pullback random attractor such that \( A(\omega) \subset B_0(\omega) \).

**Proposition 3.1.** The pullback random attractor of system (3.3)-(3.4) consists of a singleton component given by \( A(\omega) = \{ (0, 0) \} \) as long as
\[ \bar{D} > \mu(s_{in}) \quad (3.8) \]
holds true.

**Proof.** We would like to note that the result in this proposition follows trivially if \( \sigma \) remains always positive (Case 1 in the proof of Theorem 3.1) since in that case both \( \sigma \) and \( \kappa \) are positive and \( \sigma + \kappa \) tends to zero when \( t \) goes to infinity, thus the pullback random attractor is directly given by \( A(\omega) = \{ (0, 0) \} \).

Due to the previous reason, we will only present the proof when there exists some \( t^* > 0 \) such that \( \sigma(t^*) = 0 \), which implies that \( \sigma(t) < 0 \) for all \( t > t^* \). Hence, since \( \mu(s) = ms/(a + s) \), from (3.4) we have
\[ \frac{d\kappa}{dt} \leq -(\bar{D} + \alpha z^*)\kappa + \frac{ms_{in}}{a + s_{in}} \kappa, \]
which allows us to state the following inequality
\[ \kappa(t; t^*, \theta_{-\omega}, \kappa(t^*)) \leq \kappa(t^*)e^{-\left(\bar{D} - \frac{ms_{in}}{a + s_{in}}\right)(t-t^*) - \alpha \int_{t^*}^{t} z^*(\theta_s)ds}, \quad (3.9) \]
where the right side of (3.9) tends to zero when \( t \) goes to infinity, as long as (3.8) is fulfilled. Therefore \( A(\omega) = \{ (0, 0) \} \).

Finally, defining the mapping \( T : \Omega \times \bar{X} \rightarrow \bar{X} \) by
\[ T(\omega, \zeta) = \left( (\zeta_1 - s_{in})e^{\alpha z^*(\omega)}, \zeta_2e^{\alpha z^*(\omega)} \right), \]
it is a homeomorphism whose inverse is given by the following expression
\[ T^{-1}(\omega, \zeta) = \left( s_{in} + \zeta_1 e^{-\alpha z^*(\omega)}, \zeta_2 e^{-\alpha z^*(\omega)} \right). \]
If we now define
\[ \varphi_v(t, \omega) v_0 := T^{-1}(\theta_t \omega, \varphi_u(t, \omega) T(\omega, v_0)) \]
\[ = T^{-1}(\theta_t \omega, u(t; 0, \omega, u_0)) \]
\[ = v(t; 0, \omega, v_0) \]
by Proposition 4.2 it turns out that \( \varphi_v \) is the RDS associated to the stochastic chemostat model (3.1)-(3.2) with pullback random attractor \( \hat{A}(\omega) \subset \hat{B}_0(\omega) \), where
\[ \hat{B}_0(\omega) := \{ (s, x) \in \tilde{X} : s + x = s_{in}, s \geq -a \} \] (3.10)

In addition, under (3.8), the pullback random attractor for (3.1)-(3.2) reduces to a singleton set \( \hat{A}(\omega) = \{ (s_{in}, 0) \} \), which means that the microorganisms become extinct.

We remark that it is not possible to provide conditions which ensure the persistence of the microbial biomass even though our numerical simulations show that we obtain it for many different values of the parameters involved in the system, as we will present in Section 4. Moreover, we will also compare the numerical simulations concerning this section with those corresponding to the previous one.

4. Numerical simulations and final comments. In this section we would like to highlight some comments about both ways of modeling stochasticity and randomness in a chemostat model and show some numerical simulations which will support the results proved throughout Sections 2 and 3.

We remark that we use the Euler-Maruyama method which is a simple generalization of the Euler method for ODEs to stochastic differential equations. The main difference is the discretization of the term \( dW(t) = W(\tau_j) - W(\tau_{j-1}) \) for some partition \( \{ \tau_j \} \) of the time interval, where we make use of the fact that such a difference is a Gaussian variable with mean zero and variance \( \tau_j - \tau_{j-1} \). For more detailed information about the definition of the numerical scheme necessary to obtain the numerical simulations we refer the readers to [7, 8, 9, 20].

In every simulation, the dashed lines represent the solution of the deterministic systems, i.e., the behavior of the stochastic/random system after taking \( \alpha = 0 \), whereas the continuous lines correspond to different realizations of the solution of the corresponding stochastic/random system.

Now, we will show some simulations concerning the random chemostat model studied in Section 2. In each of the following figures three panels are displayed: the left one shows the phase plane and the general dynamics of the chemostat model; the two panels on the right side help us to see two important zones in the phase plane.

In Figure 7 we set \( D = 2, s_{in} = 4, a = 0.6, m = 5, \alpha = 0.5, \beta = 1, \nu = 0.7 \) and initial values \( s(0) = 2, x(0) = 5 \) for the nutrient and the microorganism, respectively. In this case (2.11) holds true and this is the reason why we can observe the persistence of the species. We can also see how the realizations are approaching the line \( s + x = s_{in} \), as proved in (2.8).

In contrast to the last case, in Figure 8 we take \( D = 3.5, s_{in} = 2, a = 0.8, m = 0.5, \alpha = 0.5, \beta = 1, \nu = 0.7 \) and initial values \( s(0) = 2.5, x(0) = 5 \) for the nutrient and the microorganisms, respectively. Then we can see that the microorganisms extinguish what is not surprising due to the fact that condition (2.10) is fulfilled.
We can also see here how the realizations are approaching the line $s + x = s_{in}$, as proved in (2.8).

The simulations in Figure 9 represent the stochastic chemostat analyzed in Section 3, where the dilution rate is perturbed by a white noise. On the one hand, in the left picture we take $D = 3.5$, $s_{in} = 1$, $a = 0.8$, $m = 1.5$ and $\alpha = 0.5$. In this case, condition (3.8) is fulfilled so we can observe that the microorganisms become extinct. On the other hand, in the right picture we choose $D = 2$, $s_{in} = 1$, $a = 0.6$, $m = 5$ and $\alpha = 0.5$. In this second case $D < \mu(s_{in})$ holds, then we can see that the species persist even though it is not possible to prove mathematically the persistence. In addition, we can also see that some realizations in the right picture take negative values which is another significant drawback.

Next we present two figures where we overlap a typical realization of the solution of system (3.1)-(3.2) and another one of the solution of system (2.4)-(2.5) such that we can notice much more easily the differences between the simulations concerning Sections 2 and 3. In each figure we plot a big panel where the general dynamics can be seen and four smaller panels which correspond to two different zooms of two interesting places of the realizations, the dynamics around $(s, x) = (2, 2)$ and
Figure 9. Stochastic chemostat model. Extinction (left) and persistence (right)

Figure 10. Comparison in case of extinction

\((s, x) = (2, 0)\) in Figure 10 and the dynamics about \((s, x) = (0.2, 5.5)\) and \((s, x) = (0.4, 3.75)\) in Figure 11.

In Figure 10 we plot a typical realization when perturbing the dilution rate with the Wiener process (orange) and two different ones when perturbing with the O-U process for \(\beta = 2\) (red) and \(\beta = 0.5\) (green). In this case, we take \(s_{in} = 2, D = 3.5, a = 0.8, m = 0.5, \alpha = 0.8, \sigma = 0.8, x(0) = 5\) and \(s(0) = 2.5\). We can observe that (2.10) and (3.8) are both fulfilled then the microorganisms become extinct, as we already proved in previous sections.

Eventually, in Figure 11 we plot again a typical realization when perturbing the dilution rate with the Wiener process (orange) and two different ones when perturbing with the O-U process for \(\beta = 2\) (red) and \(\beta = 0.5\) (green) but now we take \(s_{in} = 4, D = 2, a = 0.6, m = 5, \alpha = 0.15, \sigma = 0.8, x(0) = 5\) and \(s(0) = 2\). In this case (3.8) does not hold true, thus it is not possible to ensure the persistence of the species (in the chemostat model perturbed by using the standard Wiener process) although numerically it can be obtained for the previous values of the parameters. In addition, if \(D < \mu(s_{in})\) and \(\bar{s} < s_{in}\) hold true, then we can ensure the persistence of the microbial biomass when perturbing the chemostat
model by means of the O-U process. Moreover, we can observe that every realization is approaching the line $s + x = s_{in}$, as proved in Sections 2 (see (2.16)) and 3 (see (3.10)).

In conclusion, we can observe that the Ornstein-Uhlenbeck process provides us a really useful tool when modeling stochasticity and randomness since it allows us to set up mathematical models which guarantee the positiveness of the variable and therefore it better suits to represent reality. This new framework could also allow us to revisit the persistence of species under input disturbances, in case of competition between several species, which will be the topic of a future work.

Appendix. Although very good references (see e.g. [2]) providing very detailed information about random dynamical systems (RDSs) can be found in the literature, we recall briefly some useful definitions and results to make our presentation as much self-contained as possible.

Let $(X, \| \cdot \|_X)$ be a separable Banach space.

**Definition 4.1.** An RDS on $\mathcal{X}$ consists of two ingredients: (a) a metric dynamical system $(\Omega, \mathcal{F}, P, \{\theta_t\}_{t \in \mathbb{R}})$ where $(\Omega, \mathcal{F}, P)$ is a probability space and a family of mappings $\theta_t : \Omega \to \Omega$ satisfying

1. $\theta_0 = \text{Id}_\Omega$,
2. $\theta_s \circ \theta_t = \theta_{s+t}$ for all $s, t \in \mathbb{R}$,
3. the mapping $(t, \omega) \mapsto \theta_t \omega$ is measurable,
4. the probability measure $P$ is preserved by $\theta_t$, i.e., $\theta_t P = P$

and (b) a mapping $\varphi : [0, \infty) \times \Omega \times \mathcal{X} \to \mathcal{X}$ which is $(\mathcal{B}[0, \infty) \times \mathcal{F} \times \mathcal{B}(\mathcal{X}), \mathcal{B}(\mathcal{X}))$-measurable, such that for each $\omega \in \Omega$,

- i) the mapping $\varphi(t, \omega) : \mathcal{X} \to \mathcal{X}, x \mapsto \varphi(t, \omega)x$ is continuous for every $t \geq 0$,
- ii) $\varphi(0, \omega)$ is the identity operator on $\mathcal{X}$,
- iii) (cocycle property) $\varphi(t+s, \omega) = \varphi(t, \theta_s \omega) \varphi(s, \omega)$ for all $s, t \geq 0$.

**Definition 4.2.** Let $(\Omega, \mathcal{F}, P)$ be a probability space. A random set $K$ is a measurable subset of $\mathcal{X} \times \Omega$ with respect to the product $\sigma$-algebra $\mathcal{B}(\mathcal{X}) \times \mathcal{F}$. Moreover
$K$ will be said a closed or a compact random set if $K(\omega) = \{x : (x, \omega) \in K\}$, $\omega \in \Omega$, is closed or compact for $P$–almost all $\omega \in \Omega$, respectively.

**Definition 4.3.** A bounded random set $K(\omega) \subset \mathcal{X}$ is said to be tempered with respect to $\{\theta_t\}_{t \in \mathbb{R}}$ if for a.e. $\omega \in \Omega$,

$$
\lim_{t \to \infty} e^{-\beta t} \sup_{x \in K(\theta_t \omega)} \|x\| \chi = 0, \quad \text{for all } \beta > 0;
$$

a random variable $\omega \mapsto r(\omega) \in \mathbb{R}$ is said to be tempered with respect to $\{\theta_t\}_{t \in \mathbb{R}}$ if for a.e. $\omega \in \Omega$,

$$
\lim_{t \to \infty} e^{-\beta t} \sup_{t \in \mathbb{R}} |r(\theta_t \omega)| = 0, \quad \text{for all } \beta > 0.
$$

In what follows we use $\mathcal{E}(\mathcal{X})$ to denote the set of all tempered random sets of $\mathcal{X}$.

**Definition 4.4.** A random set $B(\omega) \subset \mathcal{X}$ is called a random absorbing set in $\mathcal{E}(\mathcal{X})$ if for any $E \in \mathcal{E}(\mathcal{X})$ and a.e. $\omega \in \Omega$, there exists $T_E(\omega) > 0$ such that

$$
\varphi(t, \theta^{-t} \omega) E(\theta^{-t} \omega) \subset B(\omega), \quad \text{for all } t \geq T_E(\omega).
$$

**Definition 4.5.** Let $\{\varphi(t, \omega)\}_{t \geq 0, \omega \in \Omega}$ be an RDS over $(\Omega, \mathcal{F}, P, \{\theta_t\}_{t \in \mathbb{R}})$ with state space $\mathcal{X}$ and let $A(\omega)(\subset \mathcal{X})$ be a random set. Then $\mathcal{A} = \{A(\omega)\}_{\omega \in \Omega}$ is called a global random $\mathcal{E}$–attractor (or pullback $\mathcal{E}$–attractor) for $\{\varphi(t, \omega)\}_{t \geq 0, \omega \in \Omega}$ if

(i) (compactness) $A(\omega)$ is a compact set of $\mathcal{X}$ for any $\omega \in \Omega$;

(ii) (invariance) for any $\omega \in \Omega$ and all $t \geq 0$, it holds

$$
\varphi(t, \omega) A(\omega) = A(\theta_t \omega);
$$

(iii) (attracting property) for any $E \in \mathcal{E}(\mathcal{X})$ and a.e. $\omega \in \Omega$,

$$
\lim_{t \to \infty} \text{dist}_{\mathcal{X}}(\varphi(t, \theta^{-t} \omega) E(\theta^{-t} \omega), A(\omega)) = 0,
$$

where $\text{dist}_{\mathcal{X}}(G, H) = \sup_{g \in G} \inf_{h \in H} \|g - h\|_{\mathcal{X}}$ is the Hausdorff semi-metric for $G, H \subseteq \mathcal{X}$.

**Proposition 4.1.** [See [14, 17]] Let $B \in \mathcal{E}(\mathcal{X})$ be a closed absorbing set for the continuous RDS $\{\varphi(t, \omega)\}_{t \geq 0, \omega \in \Omega}$ that satisfies the asymptotic compactness condition for a.e. $\omega \in \Omega$, i.e., each sequence $x_n$ in $\varphi(t_n, \theta^{-t_n} \omega) B(\theta^{-t_n} \omega)$ has a convergent subsequence in $\mathcal{X}$ when $t_n \to \infty$. Then $\varphi$ has a unique global random attractor $\mathcal{A} = \{A(\omega)\}_{\omega \in \Omega}$ with component subsets

$$
A(\omega) = \bigcap_{\tau \geq T_B(\omega)} \bigcup_{t \geq \tau} \varphi(t, \theta^{-t} \omega) B(\theta^{-t} \omega).
$$

**Remark 4.1.** When the state space $\mathcal{X} = \mathbb{R}^d$ as in this paper, the asymptotic compactness follows trivially.

The next result ensures when two RDSs are conjugated (see [10, 11, 12]).

**Proposition 4.2.** Let $\varphi_u$ be an RDS on $\mathcal{X}$. Suppose that the mapping $T : \Omega \times \mathcal{X} \to \mathcal{X}$ possesses the following properties: for fixed $\omega \in \Omega$, $T(\omega, \cdot)$ is a homeomorphism on $\mathcal{X}$, and for $x \in \mathcal{X}$, the mappings $T(\cdot, x)$, $T^{-1}(\cdot, x)$ are measurable. Then the mapping

$$
(t, \omega, x) \to \varphi_u(t, \omega) x := T^{-1}(\theta_t \omega, \varphi_u(t, \omega) T(\omega, x))
$$

is a (conjugated) RDS.
REFERENCES

[1] S. Al-azzawi, J. Liu and X. Liu, Convergence rate of synchronization of systems with additive noise, Discrete Contin. Dyn. Syst. Ser. B, 22 (2017), 227–245.

[2] L. Arnold, Random Dynamical Systems, Springer Berlin Heidelberg, 1998.

[3] J. Barlow, W. Schaffner, F. de Noyelles, B. Peterson and J. Peterson, Continuous Flow Nutrient Bioassays with Natural Phytoplankton Populations, G. Glass (Editor): Bioassay Techniques and Environmental Chemistry, John Wiley & Sons Ltd., 1973.

[4] F. Campillo, M. Joannides and I. Larramendy-Valverde, Stochastic modeling of the chemostat, Ecological Modelling, 222 (2011), 2676–2689.

[5] F. Campillo, M. Joannides and I. Larramendy-Valverde, Approximation of the Fokker–Planck equation of the stochastic chemostat, Mathematics and Computers in Simulation, 99 (2014), 37–53.

[6] F. Campillo, M. Joannides and I. Larramendy-Valverde, Analysis and approximation of a stochastic growth model with extinction, Methodology and Computing in Applied Probability, 18 (2016), 499–515.

[7] T. Caraballo, M. J. Garrido-Atienza and J. López-de-la-Cruz, Some aspects concerning the dynamics of stochastic chemostats, Advances in Dynamical Systems and Control, 227–246, Stud. Syst. Decis. Control, 69, Springer, [Cham], 2016.

[8] T. Caraballo, M. J. Garrido-Atienza and J. López-de-la-Cruz, Dynamics of some stochastic chemostat models with multiplicative noise, Communications on Pure and Applied Analysis, 16 (2017), 1893–1914.

[9] T. Caraballo, M. J. Garrido-Atienza, J. López-de-la-Cruz and A. Rapaport, Corrigendum to “Some aspects concerning the dynamics of stochastic chemostats”, 2017, arXiv:1710.00774 [math.DS].

[10] T. Caraballo, M. J. Garrido-Atienza, B. Schmalfuss and J. Valero, Asymptotic behavior of a stochastic semilinear dissipative functional equation without uniqueness of solutions, Discrete and Continuous Dynamical Systems - Series B, 14 (2010), 439–455.

[11] T. Caraballo and X. Han, Applied Nonautonomous and Random Dynamical Systems, Applied Dynamical Systems, Springer International Publishing, 2016.

[12] T. Caraballo, P. E. Kloeden and B. Schmalfuss, Exponentially stable stationary solutions for stochastic evolution equations and their perturbation, Applied Mathematics and Optimization, 50 (2004), 183–207.

[13] T. Caraballo and K. Lu, Attractors for stochastic lattice dynamical systems with a multiplicative noise, Front. Math. China, 3 (2008), 317–335.

[14] T. Caraballo, G. Łukaszewicz and J. Real, Pullback attractors for asymptotically compact non-autonomous dynamical systems, Nonlinear Analysis: Theory, Methods & Applications, 64 (2006), 484–498.

[15] I. F. Creed, D. M. McKnight, B. A. Pellerin, M. B. Green, B. A. Bergamaschi, G. R. Aiken, D. A. Burns, S. E. G. Findlay, J. B. Shanley, R. G. Stiegel, B. T. Aulenbach, D. W. Clow, H. Laudon, B. L. McGlynn, K. J. McGuire, R. A. Smith and S. M. Stackpoole, The river as a chemostat: Fresh perspectives on dissolved organic matter flowing down the river continuum, Canadian Journal of Fisheries and Aquatic Sciences, 72 (2015), 1272–1285.

[16] G. D’Ans, P. Kokotovic and D. Gottlieb, A nonlinear regulator problem for a model of biological waste treatment, IEEE Transactions on Automatic Control, 16 (1971), 341–347.

[17] F. Flandoli and B. Schmalfuss, Random attractors for the 3D stochastic navier-stokes equation with multiplicative white noise, Stochastics and Stochastic Reports, 59 (1996), 21–45.

[18] J. Grasman, M. D. Gee and O. A. V. Herwaarden, Breakdown of a chemostat exposed to stochastic noise, Journal of Engineering Mathematics, 53 (2005), 291–300.

[19] J. Harmand, C. Lobry, A. Rapaport and T. Sari, The Chemostat: Mathematical Theory of Micro-organisms Cultures, Wiley, Chemical Engineering Series, John Wiley & Sons, Inc., 2017.

[20] D. J. Higham, An algorithmic introduction to numerical simulation of stochastic differential equations, SIAM Review, 43 (2001), 525–546.

[21] S. B. Hsu, S. Hubbell and P. Waltman, A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms, SIAM Journal on Applied Mathematics, 32 (1977), 366–383.

[22] L. Imhof and S. Walcher, Exclusion and persistence in deterministic and stochastic chemostat models, Journal of Differential Equations, 217 (2005), 26–53.
[23] H. W. Jannasch, Steady state and the chemostat in ecology, *Limnology and Oceanography*, 19 (1974), 716–720.
[24] J. Kalff and R. Knoechel, Phytoplankton and their dynamics in oligotrophic and eutrophic lakes, *Annual Review of Ecology and Systematics*, 9 (1978), 475–495.
[25] J. W. M. La Rivière, Microbial ecology of liquid waste treatment, in *Advances in Microbial Ecology*, vol. 1, Springer US, 1977, 215–259.
[26] E. Rurangwa and M. C. J. Verdegem, Microorganisms in recirculating aquaculture systems and their management, *Reviews in Aquaculture*, 7 (2015), 117–130.
[27] H. L. Smith and P. Waltman, *The Theory of the Chemostat: Dynamics of Microbial Competition*, Cambridge University Press, 1995.
[28] L. Wang and D. Jiang, Periodic solution for the stochastic chemostat with general response function, *Physica A: Statistical Mechanics and its Applications*, 486 (2017), 378–385.
[29] L. Wang, D. Jiang and D. O’Regan, The periodic solutions of a stochastic chemostat model with periodic washout rate, *Communications in Nonlinear Science and Numerical Simulation*, 37 (2016), 1–13.
[30] C. Xu and S. Yuan, An analogue of break-even concentration in a simple stochastic chemostat model, *Applied Mathematics Letters*, 48 (2015), 62–68.
[31] C. Xu, S. Yuan and T. Zhang, Asymptotic behavior of a chemostat model with stochastic perturbation on the dilution rate, *Abstract and Applied Analysis*, 2013 (2013), Art. ID 423154, 11 pp.
[32] D. Zhao and S. Yuan, Critical result on the break-even concentration in a single-species stochastic chemostat model, *Journal of Mathematical Analysis and Applications*, 434 (2016), 1336–1345.
[33] D. Zhao and S. Yuan, Break-even concentration and periodic behavior of a stochastic chemostat model with seasonal fluctuation, *Communications in Nonlinear Science and Numerical Simulation*, 46 (2017), 62–73.

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