

Noise Induced Phenomena in the Dynamics of Two Competing Species

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Abstract. Noise through its interaction with the nonlinearity of the living systems can give rise to counter-intuitive phenomena. In this paper we shortly review noise induced effects in different ecosystems, in which two populations compete for the same resources. We also present new results on spatial patterns of two populations, while modeling real distributions of anchovies and sardines. The transient dynamics of these ecosystems are analyzed through generalized Lotka-Volterra equations in the presence of multiplicative noise, which models the interaction between the species and the environment. We find noise induced phenomena such as quasi-deterministic oscillations, stochastic resonance, noise delayed extinction, and noise induced pattern formation. In addition, our theoretical results are validated with experimental findings. Specifically the results, obtained by a coupled map lattice model, well reproduce the spatial distributions of anchovies and sardines, observed in a marine ecosystem. Moreover, the experimental dynamical behavior of two competing bacterial populations in a meat product and the probability distribution at long times of one of them are well reproduced by a stochastic microbial predictive model.

Keywords and phrases: noise induced phenomena, population dynamics, Langevin equation, multiplicative noise, stochastic resonance, predictive microbiology

Mathematics Subject Classification: 82C05, 82C31, 60H10, 34F15, 92D25, 92D40

1. Introduction

During last years, theoreticians worked to devise deterministic mathematical models able to describe ecosystems in which chaotic dynamics and spatial patterns are present. However, due to their deterministic nature these models cannot reproduce or explain the effects of random fluctuations, which come from the intrinsic stochastic nature of open systems. Natural systems indeed are a typical example of open systems due to the continuous presence of deterministic and stochastic forces coming from the environment, which affect the dynamics of these systems.

More recently, the role of noise in population dynamics has been the subject of several theoretical studies [6, 11, 20–22, 24, 25, 27, 30, 41, 42, 44, 49, 50, 62–64, 67, 69, 70, 72, 76, 77, 86, 88, 89, 93]. Thus the study of the effects of noise is now a well established subject in several different disciplines ranging from physics, to chemistry and biology [36, 52, 58, 60, 87]. However, the essential role of the noise in theoretical ecology has been recently recognized. Some key questions in population ecology are related to the comprehension of the role that noise, climatic forcing and nonlinear interactions among individuals of the same or different species play on the dynamics of the ecosystems [11, 24, 25, 27, 86, 93]. Recently researchers devoted more interest and attention to explain the role of noise in different fields of biology [6, 10, 16, 19, 21, 22, 29, 32, 33, 39, 41, 43, 44, 68, 80, 84, 89], while investigating noise induced effects in population dynamics [20, 49, 50, 69, 70, 72].

In particular several works have studied the effects of random fluctuations on the stability of ecological systems [11, 93], showing the presence of counterintuitive phenomena, such as noise enhanced stability [1, 28, 55, 73, 74], stochastic resonance [32, 34, 51, 54, 56], and noise delayed extinction [20, 49, 69–71, 81]. The origin of these effects is the interplay between nonlinear interactions typical for natural systems and random fluctuations coming from environment due to their intrinsic characteristic of open systems. The permanent presence of noise and nonlinear interaction in population dynamics causes indeed an increase of complexity compared to other noise-driven systems, such as financial markets [14, 15, 75, 83], or many physical and chemical processes described by deterministic dynamics [68].

Therefore the intrinsic nonlinearity can cause ecological systems to critically depend on initial conditions, and both deterministic and random perturbations coming from the environment. As a consequence, the understanding of the role played by the noise in the dynamics of nonlinear systems is a crucial point for a deeper comprehension and successful modeling of the open systems governed by nonlinear dynamics, which are known as complex systems.

Moreover we recall that the study of spatial distributions of species densities is a major element to get a correct description in population dynamics. An accurate analysis of spatio-temporal patterns represents in fact a crucial point to devise predictive models. As a consequence the comprehension of the role played by the simultaneous presence of random fluctuations, deterministic forces and nonlinear interaction, typical for natural systems, is fundamental to effectively describe the spatio-temporal dynamics of biological populations [12, 20, 48, 49, 66, 69, 70, 72, 92]. Thus, a deeper comprehension of the role of random fluctuations in ecology underlies a better knowledge and description of real natural systems. Nevertheless, despite of the big amount of theoretical work and effort of researchers, a relevant biological issue such as the role of environmental noise in ecological systems is still widely debated.

For this purpose, we discuss here the effects of environmental noise on the dynamics of biological populations. In particular, we review some recent findings obtained for two competing species, whose dynamics is described by generalized Lotka-Volterra equations, and highlight the crucial role of the environmental noise on the dynamics of the two species. Moreover we present new results (see Section 3), obtained by a coupled map lattice model, which reproduce the spatial distributions of two fish populations, i.e. anchovies and sardines. Our analysis focus on three different ecosystems, in which external random

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fluctuations are modeled by terms of multiplicative noise [6, 21, 22]. As a result we find that: (a) in a single compartment ecosystem the presence of a driving force causes stochastic resonance, which results in quasi-periodic oscillations of the two population densities; b) in the same ecosystem it is possible to observe a nonmonotonic behavior of the average extinction time of one species as a function of the noise intensity, i.e. noise delayed extinction; (c) a two-dimensional spatio-temporal model is able to reproduce the concentrations of two fish species in a real marine ecosystem located in the Mediterranean Sea; (d) in a food product the presence of randomly fluctuating environmental variables such as temperature, pH, and available water is taken into account in modeling the growth of two bacterial populations, while allowing to obtain a better agreement between experimental data and theoretical results compared to the corresponding deterministic approach.

2. Stochastic dynamics of two competing species: single compartment model

In this section we study the effect of random fluctuations in the dynamics of two competing species. The model consists of generalized Lotka-Volterra equations with terms of multiplicative noise, which mimics the random fluctuations of environmental variables. The two populations, x and y , interact through the term $-\beta xy$, where β is the coupling constant, which regulates the interaction strength and is a stochastic process. More in detail the interaction coefficient $\beta(t)$ can be represented as a virtual particle moving along a bistable potential and subject to both a periodic driving term, which models seasonal changes in temperature, and a term of additive noise which describes the effects due to the noisy behaviour of the environment.

2.1. The model

The stochastic dynamics of our ecosystem is given by the two following generalized Lotka-Volterra equations [53, 90]

$$\frac{dx}{dt} = \mu_1 x (\alpha_1 - x - \beta_1(t)y) + x \xi_x(t) \quad (2.1)$$

$$\frac{dy}{dt} = \mu_2 y (\alpha_2 - y - \beta_2(t)x) + y \xi_y(t), \quad (2.2)$$

which are stochastic differential equations in Ito sense, with $\xi_x(t)$ and $\xi_y(t)$ statistically independent Gaussian white noises with zero mean and correlation function $\langle \xi_i(t)\xi_j(t') \rangle = \sigma\delta(t-t')\delta_{ij}$ ($i, j = x, y$), and σ the multiplicative noise intensity. To get the time evolution for the two species densities the parameters are set as follows: $\alpha_1 = \alpha_2 = \alpha$, $\beta_1(t) = \beta_2(t) = \beta(t)$. We recall that $\beta < 1$ determines the coexistence regime (both species survives), while $\beta > 1$ corresponds to the exclusion regime (one of the two species disappears after some time). Coexistence and exclusion of one of the two species represent indeed stable states of the Lotka-Volterra's deterministic model [7]. As previously said, natural systems are affected by a continuous exchange with a noisy nonstationary environment. This implies that also the interaction parameter is subject to both random fluctuations and deterministic external signal such as the periodical changes in temperature. The competition rate $\beta(t)$, continuously varying between exclusion and coexistence regime due the interplay between two main factors such as limiting resources and noisy environment, is responsible for a random competition between the two populations. As a consequence, the simultaneous presence of noise and periodic driving causes the system to pass from a dynamical regime ($\beta < 1$, coexistence) to the other one ($\beta > 1$, exclusion) and vice versa. This random process can be described by an Ito stochastic differential equation, which reproduces, as previously noted, the dynamics of a virtual particle moving along a bistable potential, in the presence of a periodical driving force and an additive noise term

$$\frac{d\beta(t)}{dt} = -\frac{dU(\beta)}{d\beta} + \gamma\cos(\omega_0 t) + \xi_\beta(t), \quad (2.3)$$

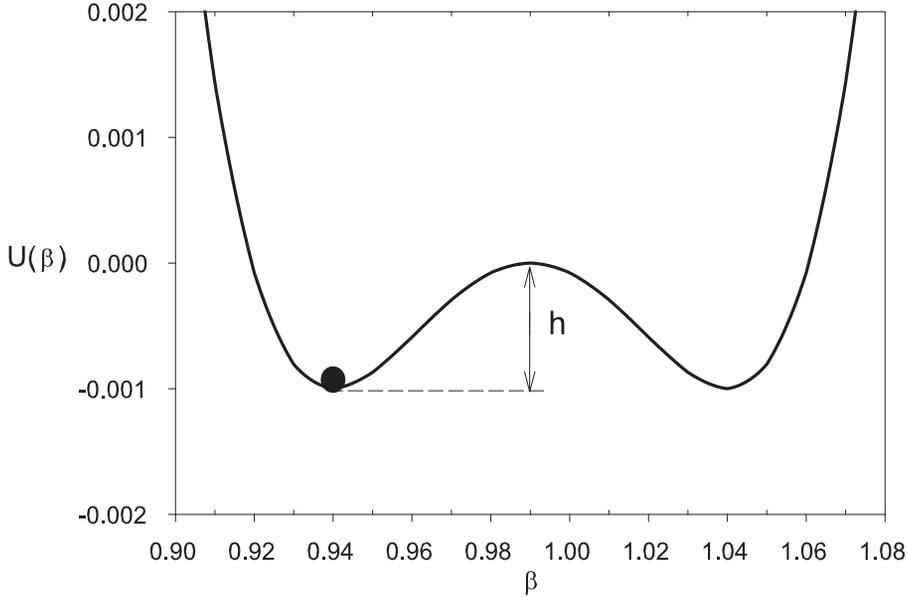


FIGURE 1. The bistable potential $U(\beta)$ of the interaction parameter $\beta(t)$. The potential $U(\beta)$ is centered on $\beta = 0.99$. The parameters of the potential are $h = 6.25 \cdot 10^{-3}$, $\eta = 0.05$, $\rho = -0.01$.

where $U(\beta)$ is the bistable potential shown in Fig. 1 and given by

$$U(\beta) = h(\beta - (1 + \rho))^4/\eta^4 - 2h(\beta - (1 + \rho))^2/\eta^2, \quad (2.4)$$

Here h is the height of the potential barrier. The periodic term account for seasonal variations of environmental temperature, with $\gamma = 10^{-1}$ and $\omega_0/(2\pi) = 10^{-3}$. In Eq. (2.3) $\xi_\beta(t)$ is a Gaussian white noise with the usual statistical properties $\langle \xi_\beta(t) \rangle = 0$ and $\langle \xi_\beta(t)\xi_\beta(t') \rangle = \sigma_\beta \delta(t - t')$, with σ_β the additive noise intensity. According to the form of the potential, one can expect that in the deterministic case ($\sigma_\beta = 0$) the coexistence regime takes place when the virtual particle (initial value of β) is placed in the left well.

2.2. Stochastic resonance

As a first step we study how the noise affects the dynamics of the two populations, whose dynamical regime is strongly dependent on the interaction parameter. Therefore we analyze the time evolution of $\beta(t)$ fixing different values of the additive noise intensity. Setting $\sigma_\beta = 0$ (deterministic regime), $\beta(t)$ undergoes a periodical behavior with the system remaining in the coexistence regime (see Fig. 2a). Increasing the noise ($\sigma_\beta \ll h$) the periodical behavior appears slightly perturbed due to the presence of random fluctuations (Fig. 2c). As the noise intensity increases ($\sigma_\beta \simeq h$), the virtual particle, i.e. the value of the interaction parameter, jumps between $\beta = 0.94$ and $\beta = 1.04$, which corresponds to the coexistence ($\beta < 1$) and exclusion regime ($\beta > 1$), respectively. In Fig. 2b the typical picture of stochastic resonance is shown. However, for higher values of the noise intensity σ_β , a loss of coherence is observed and the system dynamics is mainly driven by the source of random fluctuations (see Fig. 2d). This behavior can be interpreted as a cooperation between the periodical driving of the temperature, due to some geological cause, and the environmental noise [3, 8, 9] for intermediate values of the noise intensity. In this case the noise results to be tuned with the deterministic oscillating external perturbation, causing the well known stochastic resonance phenomenon. The noise intensity, $\sigma_\beta = 1.78 \cdot 10^{-3}$, which causes the synchronization shown in Fig. 2c, can be easily obtained by the formula [45, 46] setting

$$\tau_k = T_0/2, \quad (2.5)$$

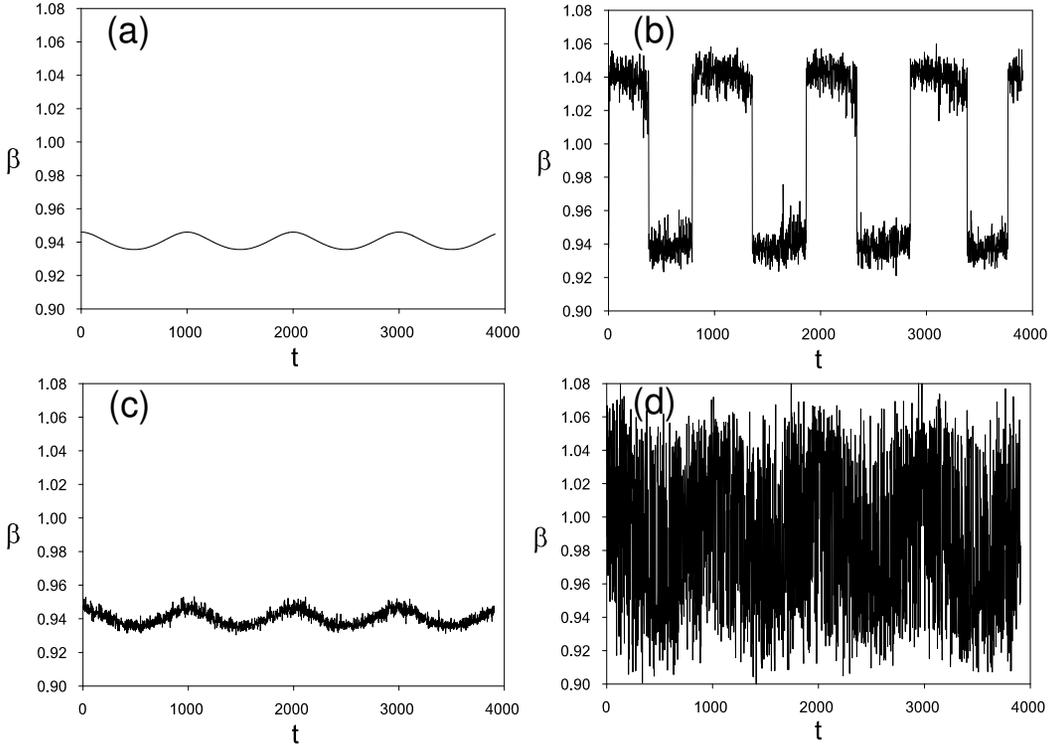


FIGURE 2. Time evolution of the interaction parameter for different values of the additive noise intensity. (a) $\sigma_\beta = 0$; (b) $\sigma_\beta = 1.78 \cdot 10^{-4}$; (c) $\sigma_\beta = 1.78 \cdot 10^{-3}$; (d) $\sigma_\beta = 1.78 \cdot 10^{-2}$. The values of the parameters are $\gamma = 10^{-1}$, $\omega_0/(2\pi) = 10^{-3}$.

where τ_k is the Kramers time [40]

$$\tau_k = \frac{2\pi}{\sqrt{|U''(0.99)|U''(0.94)}} \exp[2h/\sigma_\beta], \quad (2.6)$$

and T_0 is the period of the driving force. In Eq. (2.6) $U''(0.99)$ and $U''(0.94)$ are the second derivative calculated in the unstable and stable states of the potential, respectively. Setting $\sigma_\beta = 1.78 \cdot 10^{-3}$, which gives an alternated regime with quasi-periodical jumps between coexistence and exclusion, it is possible to get the ecosystem dynamics when the stochastic resonance (SR) condition is present, varying the magnitude σ of the multiplicative noise sources which act directly on the two species. Using as initial conditions $x(0) = y(0) = 1$, we note that, after a short transient, both populations take on the same stationary value $x_{st} = y_{st} = \alpha/(1 + \beta) \approx 1/2$, around which the population densities perform quasi-periodic oscillations whose amplitudes depend on the magnitude of the multiplicative noise.

We observe that in the absence of multiplicative noise, i.e. $\sigma = 0$ (see Fig. 3a), and for low noise intensity, i.e. $\sigma = 10^{-12}$ (see Fig. 3b), a dynamical coexistence regime characterized by correlated oscillations of the two species densities is established. We observe that this behaviour is connected with the symmetry of the Lotka-Volterra equations due to the choice of the parameter values and initial conditions (the same for the two populations). As a consequence the species undergoes correlated oscillations around the stationary value $\alpha/(1 + \beta)$ (see panels a, b of Fig. 3), even if the ecosystem, driven by the quasi-periodic behaviour of the interaction parameter (SR effect), is in the exclusion regime during the 50% of the time.

The symmetry condition is broken as the multiplicative noise intensity increases, causing the appearance of anti-correlated oscillations (see panels c, d, e of Fig. 3). The amplitude of these anti-correlated oscillations increases for higher intensity of the multiplicative noise ($\sigma = 10^{-2}$), causing a degradation of the quasi-periodical behaviour in the time series of the populations (see Fig. 3f): now the ecosystem is

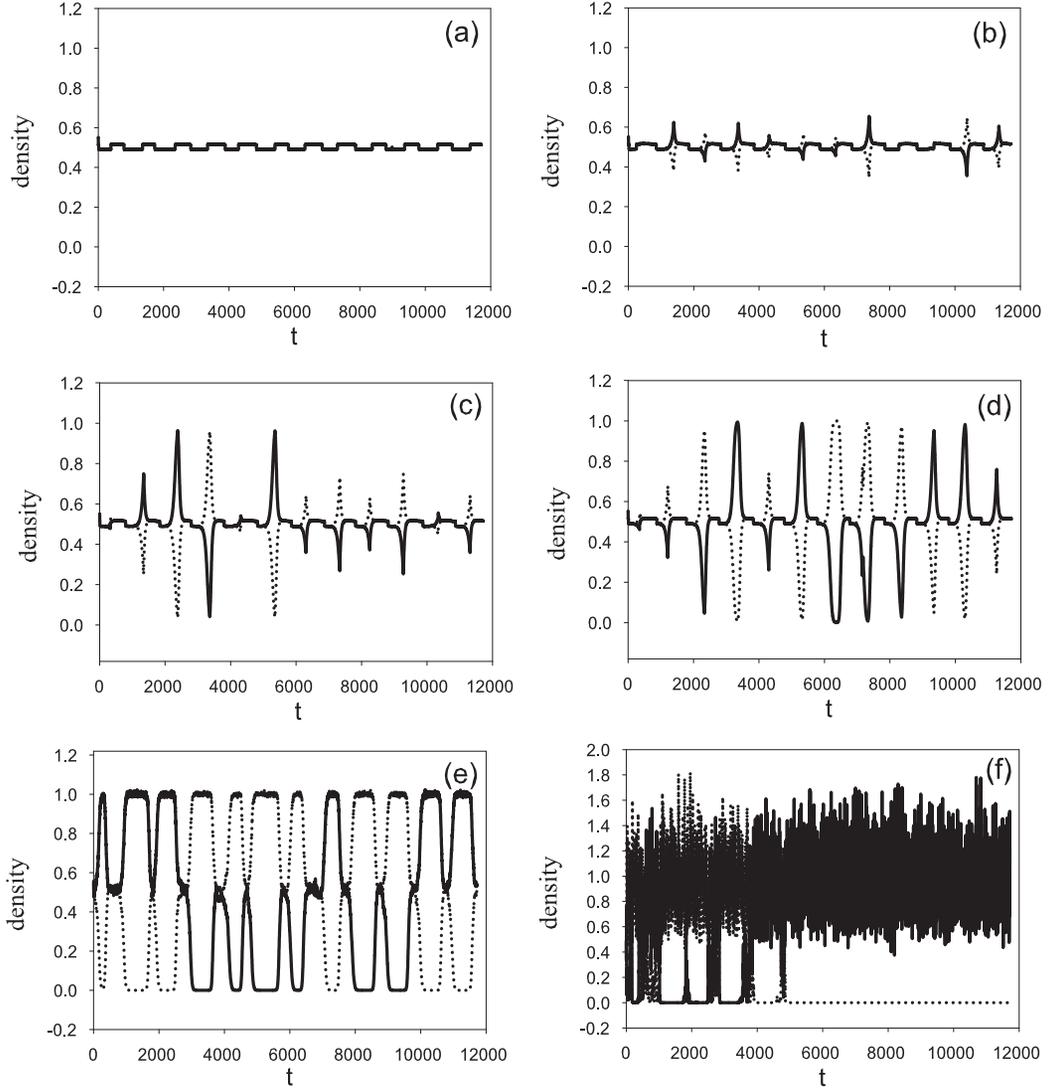


FIGURE 3. Time evolution of both populations at different levels of the multiplicative noise: (a) $\sigma = 0$; (b) $\sigma = 10^{-11}$; (c) $\sigma = 10^{-10}$; (d) $\sigma = 10^{-9}$; (e) $\sigma = 10^{-4}$; (f) $\sigma = 10^{-1}$. The values of the parameters are $\mu = 1$, $\alpha = 1$, $\gamma = 10^{-1}$, $\omega_0/2\pi = 10^{-3}$. The intensity of the additive noise is fixed at the value $\sigma_\beta = 1.78 \cdot 10^{-3}$. The initial values of the two species are $x(0) = y(0) = 1$.

mainly driven by the noise which tends to suppress the effect of the periodical signal. The presence of the multiplicative noise indeed breaks the symmetric dynamical behaviour of the ecosystem. For $\beta > 1$, i. e. in the exclusion regime, this symmetry breaking determines different behaviour in the time series of the two species: one tends to survive, while the other one tends to extinguish. Fig. 3 indicates that the effect of quasi-periodic signal can be amplified by higher intensities of the multiplicative noise. The periodicity of the noise-induced oscillations in the time behavior of the population densities shown in Fig. 3e is the same of the driving periodic term of Eq.(2.3). This is the signature of stochastic resonance phenomenon. This second SR phenomenon can be quantitatively investigated calculating the signal-to-noise ratio (SNR) of the squared difference of population densities. More exactly we consider the time series $[x(t) - y(t)]^2$ at different values of the noise intensity σ , and calculate the SNR according to Ref. [2]. This quantity is

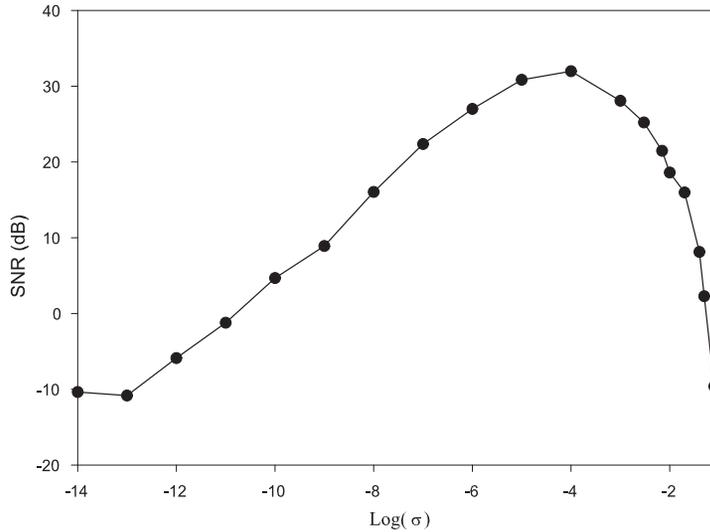


FIGURE 4. *Log-Log plot of SNR as a function of the multiplicative noise intensity. The SNR corresponds to the squared difference of population densities $(x - y)^2$. The values of the parameters are the same of Fig. 3.*

shown in Fig. 4 as a function of the multiplicative noise intensity σ , for $\sigma_\beta = 1.78 \cdot 10^{-3}$. We note that a maximum is found for $\sigma = 10^{-4}$. This indicates that the additive noise determines the conditions for the different dynamical regimes of the two species, while the multiplicative noise is responsible for a coherent response of the system, breaking the initial condition of symmetry of the ecosystem.

2.3. Noise delayed extinction

In this section we study how one of the two populations can vanish due to the interplay between the periodical signal and the additive noise $\xi_\beta(t)$, which drive the ecosystem through the two different regimes, i.e. coexistence and exclusion.

For this purpose we introduce the average extinction time of one species and calculate it for different values of the noise intensity σ_β , setting the multiplicative noise intensity at a small value, so that the dynamics is weakly perturbed by the noise and the ecosystem remains far from the SR regime. Fixing $\sigma = 10^{-9}$ and $\beta(0) = 0.94$ as initial condition, we integrate Eqs. (1) and (2) by performing 200 numerical realizations, and obtaining the behaviour of the mean extinction time (MET) of one species as a function of the additive noise intensity σ_β (see Fig. (5a)).

In these conditions, for $\sigma_\beta = 0$, the ecosystem remains in the coexistence regime, that is the deterministic extinction time of both species is infinite. By introducing noise, exclusion takes place and a finite mean extinction time (MET) appears.

We note that for small and large values of the additive noise intensity (see regions 1 and 3 in Fig. 5a), the system is in a dynamical regime which favours the coexistence of the two species, so that no extinction occurs (see time series shown in panels b and d of Fig. 5). Conversely, for intermediate values of σ_β , exclusion of one species is found with different extinction times. In particular, a minimum MET is observed for $\sigma_\beta = 2.75 \cdot 10^{-3}$, which is of the same order of magnitude of the potential barrier height h . The Kramers time corresponding to this noise intensity is $\tau_k = 41.6$, a value approximately equal to τ_{min} . This behaviour reproduces the effect of random modifications of the environmental conditions responsible for the delayed extinction of biological species in real ecosystems, as it is observed in experimental data of populations in a very long time interval [18, 35]. Starting from a situation in which one of the two population undergoes rapidly extinction (region 2 in Fig. 5a), varying the noise intensity (decrease or increase of σ_β) the ecosystem moves towards regions where the MET becomes larger (see the region between 1 and 2 and that between 2 and 3 in Fig. 5a). From a physical point of view this effect can

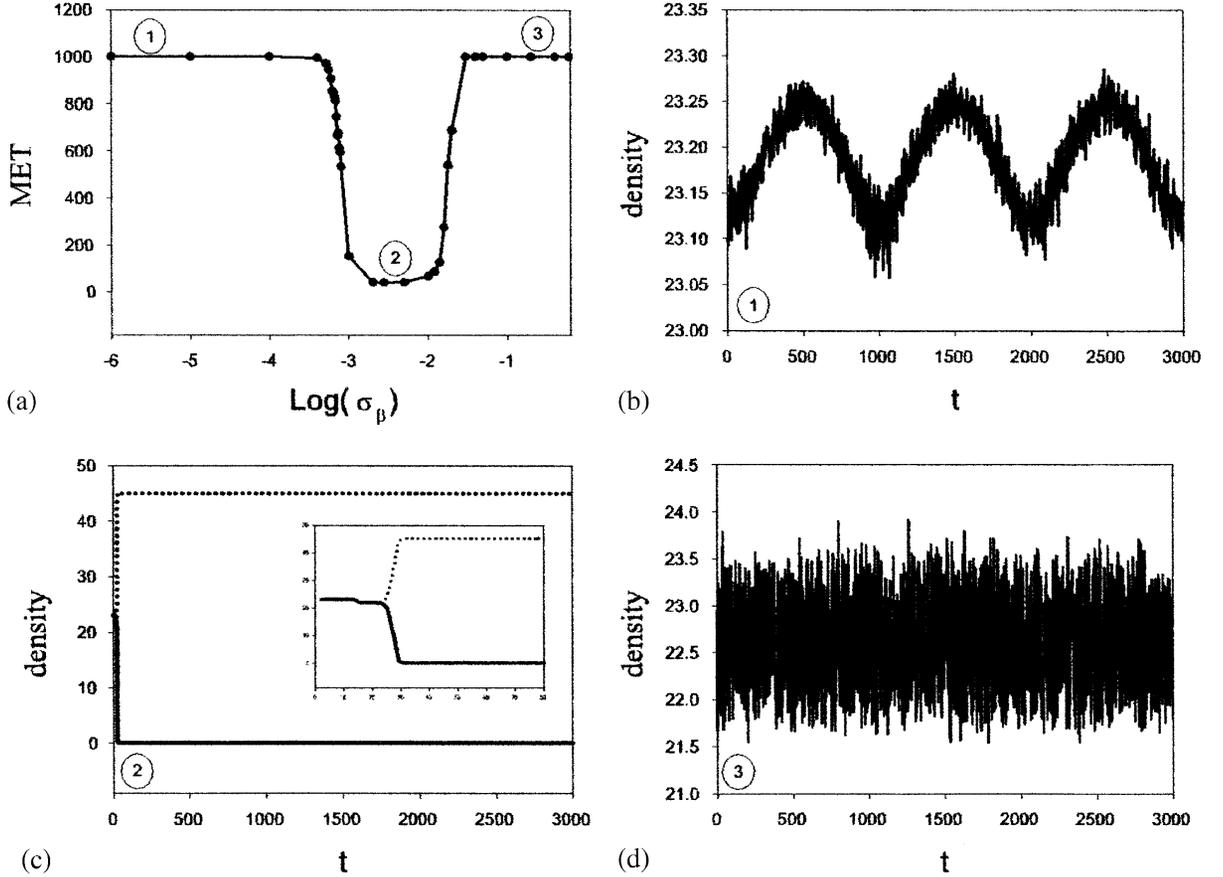


FIGURE 5. (a) Mean extinction time of one species as a function of the noise intensity σ_β . Time evolution of both species for different levels of additive noise: (b) $\sigma_\beta = 10^{-4}$, (c) $\sigma_\beta = 2 \cdot 10^{-3}$, (d) $\sigma_\beta = 10^{-1}$. The values of the parameters are $\mu = 1$, $\alpha = 45$, $\gamma = 10^{-1}$, $\omega_0/2\pi = 10^{-3}$. The intensity of the multiplicative noise is fixed at the value $\sigma = 10^{-9}$. The initial values of the two species are $x(0) = y(0) = 1$.

be explained observing that for small values of σ_β , the initial condition ($\beta(0) = 0.94$) is maintained for low noise intensity (the Kramers time is very long and the virtual particle takes very long times to cross the barrier and reach the right well corresponding to the exclusion regime). On the other side, for higher noise intensities there is a strong decrease of the Kramers time and the values of $\beta(t)$ switch very rapidly between the two wells, determining an alternate regime coexistence/exclusion which avoids the extinction. Conversely, for intermediate values of the additive noise intensity (see region 2 in Fig. 5), after an initial permanence in the left well $\beta(t)$ reaches the right well, where it remains for a time long enough to cause the extinction of one of the two species (see time series shown in panel c of Fig. 5).

3. Stochastic dynamics of two competing species: spatially extended model

In this section we consider two populations, distributed in a two-dimensional spatial domain, subject to multiplicative noise, in the presence of an external periodic signal. The multiplicative noise source mimics the effects of random fluctuations of the environmental variables.

3.1. The model

The spatio-temporal dynamics of the two populations is given by a discrete time evolution model, based on the coupled map lattice (CML) approach [47], and is the discrete version of the Lotka-Volterra equations, where diffusive terms were added [82]

$$x_{i,j}^{n+1} = \mu x_{i,j}^n (1 - x_{i,j}^n - \beta^n y_{i,j}^n) + \sqrt{\sigma_x} x_{i,j}^n X_{i,j}^n + D \sum_{\gamma} (x_{\gamma}^n - x_{i,j}^n) \quad (3.1)$$

$$y_{i,j}^{n+1} = \mu y_{i,j}^n (1 - y_{i,j}^n - \beta^n x_{i,j}^n) + \sqrt{\sigma_y} y_{i,j}^n Y_{i,j}^n + D \sum_{\gamma} (y_{\gamma}^n - y_{i,j}^n), \quad (3.2)$$

with $x_{i,j}^n$ and $y_{i,j}^n$ densities of the two populations in the site (i,j) at the time step n . Here β^n is the interaction parameter at the same time step, μ is the growth rate, D is the diffusion constant and \sum_{γ} represents the sum over the four nearest neighbors. $X_{i,j}^n$ and $Y_{i,j}^n$ are independent Gaussian random variables with zero mean and variance unit. Moreover, σ_x and σ_y are the intensities of the two multiplicative noise sources. The interaction parameter β^n is the same stochastic process $\beta(t)$ as in previous section (see Eq. (2.3)), where $U(\beta)$ is the bistable potential shown in Fig. 1. Therefore, also in this spatially extended model the switching of $\beta(t)$ between the exclusion and coexistence regime occurs randomly. This mimics the effect of the noisy environment on limiting factors such as food resources, with the periodical force accounting for the periodical (seasonal) oscillations of temperature. According to the analysis performed for the single compartment system, the two stable states (left and right wells of the potential $U(\beta)$) correspond to coexistence and exclusion of one of the two species of the Lotka-Volterra deterministic model [20, 49, 69, 70, 72, 81].

3.2. Results

By numerical integration of Eqs. (2.3), (3.1), (3.2) we obtain the spatio-temporal evolution of the population densities for the two theoretical species. The results are given in Fig. 6. Here the spatial distribution of the species x and y are shown at a certain time in the left and right panel, respectively. Light and dark grey zones represent low and high densities, respectively. These theoretical spatial distribution are compared with real data, for anchovies and sardines, collected along the acoustic transects tracked by the Interdisciplinary Group of Oceanography of IAMC-CNR of Mazara del Vallo [13], during the oceanographic campaign "ANCHEVA '02" in the Strait of Sicily. In particular, in Fig. 6 (left panel) the anchovy abundance, estimated experimentally along the acoustic transects, from point 42 to point 50 is shown. Analogously in Fig. 6 (right panel) the sardine abundance, estimated experimentally along the same acoustic transects, is shown. White and black tracts indicate small and large values, respectively, of anchovy and sardine abundances.

Predicted results show a good qualitative agreement with the spatial distributions observed for anchovy and sardine abundances. In particular we find that, in the most of the transects considered, a higher (lower) density for species x corresponds, in the same area, to a larger (smaller) anchovy abundance. More in detail, in Fig. 6 (left panel) a good correspondence can be observed between the density of the species x and the anchovy abundance along the segments 42-43, 43-44, 45-46, 47-48, 48-49 and 49-50, with discrepancies appearing along the segments 44-45 and 46-47.

A similar situation is observed for species y and sardines. In particular, the spatial distributions of species y and sardines are shown in Fig. 6 (right panel). Here a good agreement between predicted and observed abundances can be observed along the segments 42-43, 43-44, 44-45, 45-46, 46-47, 47-48 and 49-50, with a lack of agreement along the segment 48-49.

4. Predictive microbiology

Predictive microbiology exploits mathematical models to describe bacterial dynamics in different products of food industry. The models take into account the role played by environmental variables, whose

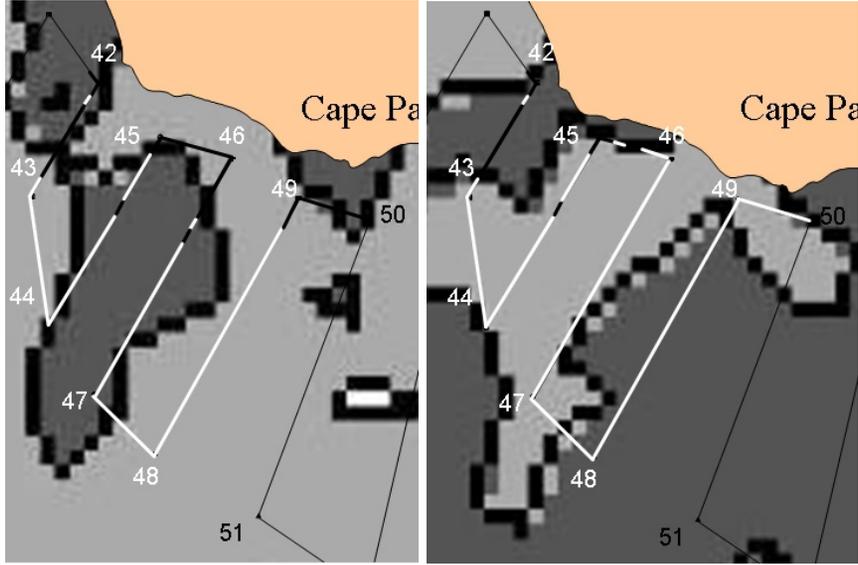


FIGURE 6. Comparison between spatial distribution of species x and anchovy abundance (left panel) and species y and sardine abundance (right panel). The values for x and y were obtained from the model at time step $n = 600$. The anchovy and sardine abundances were estimated experimentally along the acoustic transect, from point 42 to point 50, tracked during the oceanographic campaign "ANCHEVA '02" by the Interdisciplinary Group of Oceanography of IAMC-CNR of Mazara del Vallo. The spatial distribution of x and y are drawn by light and dark grey zones which represent, respectively, low and high density of the two species. The values of the parameters are $\mu = 2$, $\nu = \omega_0/(2\pi) = 0.34$, $\gamma = 10^{-5}$, $\sigma_x = \sigma_y = 10^{-8}$, $\sigma_\beta = 10^{-12}$, $D = 0.05$, $\beta(0) = 0.95$. The initial values for the spatial distributions of x and y are $x_{i,j}^{init} = y_{i,j}^{init} = 0.5$ for all sites (i, j) . Concerning the experimental distributions, white and black tracts indicate, respectively, small and large values of anchovy (left panel) and sardine (right panel) abundances estimated experimentally during the oceanographic campaign [13].

variations can affect, sometimes dramatically, the quality and safety of the food products. Predictive models belong to three different types: primary, secondary and tertiary [91]. The first class of models allows to obtain the time evolution of microbial populations. The models belonging to the second type give information on the relationship between parameters which appear in primary models, and physical and chemical variables such as T (temperature), pH (hydrogen ion concentration), and a_w (activity of water). The third class of models puts together the primary and secondary ones, letting the evolution of physical and chemical variables be considered, when analysis and prediction of the concentration of spoiling or pathogen bacteria of the food are performed [23].

A well-known method for the theoretical analysis of microbial growth exploits generalized Lotka-Volterra (LV) equations [53,90], which allow to describe the dynamics of two competing bacterial populations in different food products. A prototype model structure for mixed microbial populations in food products was proposed by Dens et al. [26]. A similar approach indicated that experimental data for *Escherichia coli* O157:H7 in ground beef could be well reproduced by an interspecific competition model for two bacterial populations. In the same work the effects of random fluctuations were considered using growth rates whose values are obtained from uniform random distributions [61]. An extensive review on predictive microbiology showed that in general a stochastic approach provides predictions which exclude the worst-case scenario [57]. In particular, stochastic terms were introduced to reproduce and predict bacterial dynamics, exploiting an approach based on primary and secondary growth models [59]. Moreover other authors presented a stochastic model which interprets the bacterial growth as the average

evolution of many cells: measured values of the growth rate for many different cells allow to describe the theoretical growth rate used in the model as a stochastic variable with a corresponding probability distribution [4, 5, 78].

The previous models however do not include explicitly stochastic terms in the equations of motion of the systems analyzed. In other words, the models used in predictive microbiology are not usually based on stochastic differential equations.

In the following we analyze how predictions for bacterial dynamics are affected by the three following features: (i) use of differential equations (dynamical approach); (ii) presence of interactions among bacterial populations; (iii) introduction of stochastic terms, i.e. noise sources, which mimic the random fluctuations of environmental variables.

4.1. Bacterial growth in meat products: single compartment dynamics of two interacting populations

In this section we introduce a model for the dynamics of two competing bacterial populations, *Listeria monocytogenes* and lactic acid bacteria (LAB), present in a meat product, i.e. a traditional Sicilian salami (Salame S. Angelo PGI (Protected Geographical Indication)) very important from the point of view of the Italian food industry. Specifically, *L. monocytogenes* is a microbial agent of foodborne disease, while LAB constitute the normal bacterial flora of the substrate. The theoretical approach is based on generalized Lotka-Volterra (LV) equations [26, 61], in which the bacterial growth rates depend on environmental variables, such as temperature, pH, and activity of water, whose randomly fluctuating behaviour can be modeled by inserting terms of additive white Gaussian noise

$$\frac{dN_{Lmo}}{dt} = \mu_{Lmo}^{max} N_{Lmo} \frac{Q_{Lmo}}{1 + Q_{Lmo}} \left(1 - \frac{N_{Lmo} + \beta_{Lmo/LAB} N_{LAB}}{N_{Lmo}^{max}} \right) \quad (4.1)$$

$$\frac{dQ_{Lmo}}{dt} = \mu_{Lmo}^{max} Q_{Lmo} \quad (4.2)$$

$$\frac{dN_{LAB}}{dt} = \mu_{LAB}^{max} N_{LAB} \frac{Q_{LAB}}{1 + Q_{LAB}} \left(1 - \frac{N_{LAB} + \beta_{LAB/Lmo} N_{Lmo}}{N_{LAB}^{max}} \right) \quad (4.3)$$

$$\frac{dQ_{LAB}}{dt} = \mu_{LAB}^{max} Q_{LAB}. \quad (4.4)$$

Here, N_{Lmo} and N_{LAB} are the population concentrations of *L. monocytogenes* and LAB, respectively; μ_{Lmo} and μ_{LAB} represent the maximum specific growth rates of the two populations, and N_{Lmo}^{max} and N_{LAB}^{max} are the theoretical maximum population concentrations. The coefficients $\beta_{Lmo/LAB}$ and $\beta_{LAB/Lmo}$ are the interspecific competition parameters of LAB on *L. monocytogenes* and vice-versa. Q_{Lmo} and Q_{LAB} represent the physiological state of the two populations.

To solve Eqs. (4.1)–(4.4) it is necessary to set how μ_{Lmo}^{max} and μ_{LAB}^{max} vary. This can be done by introducing for the maximum growth rates the following secondary model

$$\begin{aligned} \mu_{Lmo}^{max} &= 0.14776 (T_0 - 0.88) \cdot (1 - \exp(0.536 (T - 41.4))) \cdot \sqrt{aw - 0.923} \\ &\cdot \sqrt{1 - 10^{4.97 - pH}} \cdot \sqrt{1 - \frac{LAC}{3.79 (1 + 10^{pH - 3.86})} 10^{4.97 - pH} \cdot \frac{350 - NIT}{350}} \end{aligned} \quad (4.5)$$

$$\mu_{LAB}^{max} = 0.00234 (aw - 0.928) \cdot (pH - 4.24) \cdot (pH - 9.53) \cdot (T - 3.63), \quad (4.6)$$

obtained by a phenomenological approach (see Ref. [38] and references therein). Here, NIT is nitrite concentration in *ppm* and LAC is lactic acid concentration in *gl*⁻¹. The values 0.88, 41.4, 0.923, 4.97, and 350 represent T_{min} (°C), T_{max} (°C), aw_{min} , pH_{min} and NIT_{max} , respectively. Temperature, pH, and activity of water are described as stochastic processes. In particular, their dynamics is given by two different contributions: (i) a linearly decreasing deterministic behaviour within a time interval of 168 h, according to the procedure followed in the production process (a fermentation period of 7 days); (ii)

terms of additive white Gaussian noise, which account for the presence of random fluctuations due to environmental perturbations. By this way the following system of three stochastic differential equations is obtained [38]

$$\frac{dT(t)}{dt} = k_T t + \xi_T(t) \quad (4.7)$$

$$\frac{d pH(t)}{dt} = k_{pH} t + \xi_{pH}(t) \quad (4.8)$$

$$\frac{d aw(t)}{dt} = k_{aw} t + \xi_{aw}(t), \quad (4.9)$$

where $\xi_i(t)$, with $i = T, pH, aw$, are statistically independent Gaussian white noises with the following properties

$$\langle \xi_i(t) \rangle = 0 \quad (4.10)$$

$$\langle \xi_i(t) \xi_i(t') \rangle = \sigma_i \delta(t - t'), \quad (4.11)$$

and σ_i are the noise intensities. Eqs. (4.1)–(4.9) have been solved numerically within the Ito scheme, per-

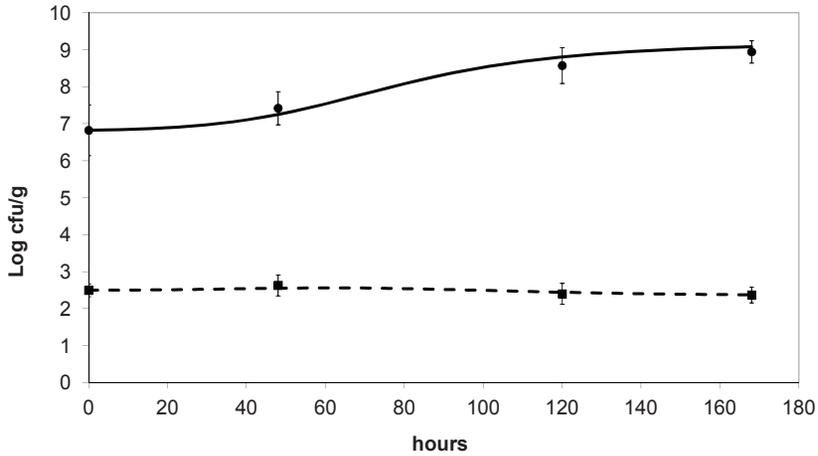


FIGURE 7. Theoretical growth curves for *L. monocytogenes* (dashed black line) and LAB (full black line), and corresponding experimental data (black squares for *L. monocytogenes*, black circles for LAB). Vertical bars indicate the experimental errors.

forming 1000 realizations and obtaining the mean growth curves in absence of noise ($\sigma_T = 0$, $\sigma_{pH} = 0$, $\sigma_{aw} = 0$). The initial concentrations of the two populations, however, have been set randomly. Specifically, in each realization the initial values of N_{Lmo} and N_{LAB} have been extracted from two Gaussian distributions, whose mean values and standard deviations were equal to those of the distributions experimentally observed [37]. The results, obtained for suitable values of the interaction parameters ($\beta_{Lmo/LAB} = 0.656$, $\beta_{LAB/Lmo} = 0$), are shown in Fig. 7. Here we note that the theoretical curves of *L. monocytogenes* (dashed black line) and LAB (full black line) fit very well the corresponding experimental data (black squares for *L. monocytogenes*, black circles for LAB). This indicates that the interaction, present in the model, between the two bacterial populations reproduces a feature of the real biological system [31, 82, 85]. In particular, we note that the condition $\beta_{LAB/Lmo} = 0$ implies the absence of any direct effects of *L. monocytogenes* on the dynamics of LAB. On the other hand, the limiting effect of LAB on the growth of *L. monocytogenes*, obtained for a suitable positive value of the other interaction parameter ($\beta_{Lmo/LAB} = 0.665$), determines conditions for the coexistence of the two populations, according to empirical data [17, 37, 79].

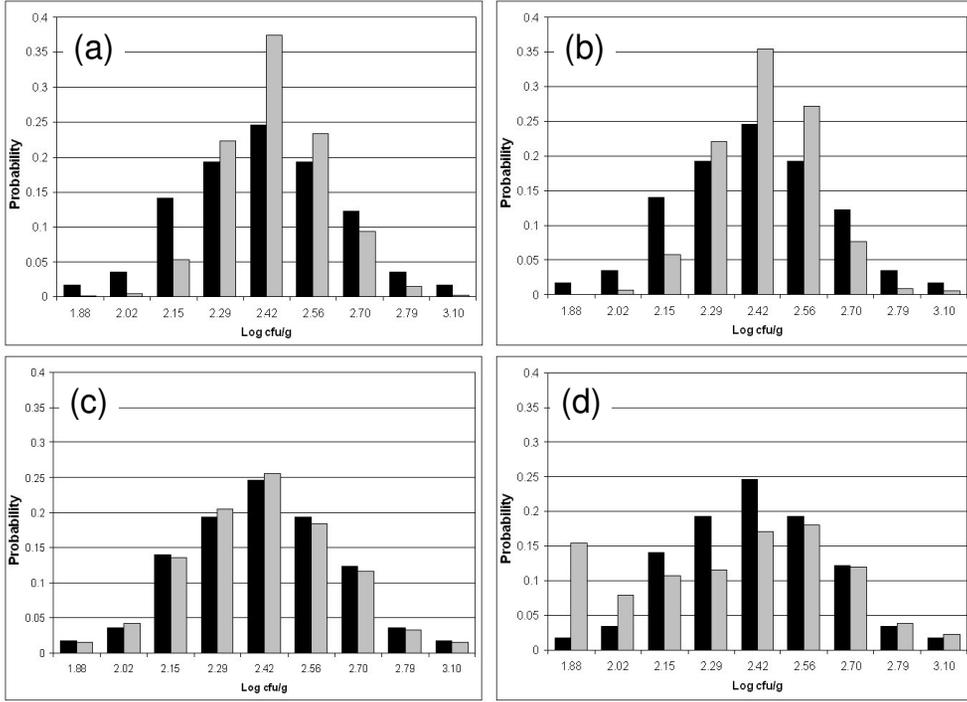


FIGURE 8. Theoretical distributions (white bars) of the *L. monocytogenes* concentration at 168 hours for (a) $\sigma_T = 0$, $\sigma_{pH} = 0$, $\sigma_{aw} = 0$, (b) $\sigma_T = 10^{-2}$, $\sigma_{pH} = 5 \cdot 10^{-4}$, $\sigma_{aw} = 10^{-5}$, (c) $\sigma_T = 2 \cdot 10^{-1}$, $\sigma_{pH} = 10^{-4}$, $\sigma_{aw} = 1.5 \cdot 10^{-4}$, (d) $\sigma_T = 5 \cdot 10^{-1}$, $\sigma_{pH} = 5 \cdot 10^{-4}$, $\sigma_{aw} = 10^{-5}$. Black bars represent the corresponding experimental distribution.

To analyze the role of the random fluctuations on the dynamics of the system, we solve Eqs. (4.1)–(4.9) both in deterministic regime and for three different values of the noise intensities σ_T , σ_{pH} and σ_{aw} . We obtain the theoretical probability distributions of *L. monocytogenes* concentration at the end of the fermentation period (168 hours). Predicted results, together with observed data, are shown in Fig. 8. Here, the histograms indicate that the best agreement between the theoretical distribution (white bars) and experimental one (black bars) is observed when the bacterial dynamics is obtained for values of the noise intensities different from zero (stochastic dynamics), and in particular for $\sigma_T = 2 \cdot 10^{-1}$, $\sigma_{pH} = 10^{-4}$, $\sigma_{aw} = 1.5 \cdot 10^{-4}$ (panel c). This result accords with the complex nature of the system analyzed, in which random fluctuations of environmental variables such as temperature, pH and activity water, are present.

5. Conclusions

In this paper we reviewed some recent results on effects of noise in the dynamics of two competing populations, whose interaction depends on a parameter β .

First we studied the dynamics of an ecosystem affected by two sources of random fluctuations: a multiplicative noise and an additive noise. The latter induces a coherent time behavior and oscillating time series of the two species densities. Moreover, an enhancement of the response of the system through stochastic resonance phenomenon is observed as a function of the multiplicative noise intensity. The model reproduces the dynamics of ecosystems subject to both deterministic oscillating changes and random modifications of environmental variables, such as variations of temperature. This interplay between the deterministic and random signals and the nonlinearity can determine a coherent response of the ecosystem. Finally, additive noise causes also a delayed extinction of one of the two populations. In particular, a

nonmonotonic behaviour of the mean extinction time, with a minimum, is found as a function of the additive noise intensity.

Afterwards we presented links between theoretical modelling in population dynamics and species distributions in two different real ecosystems consisting of two populations.

Specifically, results obtained from a discrete time evolution model were compared with those recorded for the spatial distributions of two pelagic fish populations, i.e. anchovies and sardines. The comparison showed the presence of strong correlations between theoretical and experimental distributions for both populations. These findings, previously not published, represent the novelty of the paper.

Then, we discussed a predictive microbiological model which allows to describe microbial evolution in food products as a function of environmental conditions. Our findings indicate that interspecific bacterial interaction and environmental random fluctuations are essential for a more precise and reliable prediction of the bacterial dynamics.

The noise induced phenomena discussed in this paper can contribute to understand population dynamics in ecosystems, which are complex systems due to their intrinsic nonlinearity and continuous exchange with the environment through deterministic and random perturbations [11, 18, 20, 35, 49, 69, 70, 93]. In particular, the results presented in this paper highlight the importance of including noise effects to model more effectively the dynamics of two specific real ecosystems. Indeed our results could contribute: (i) to reproduce the dynamics of fish populations and predict the effects of global warming on marine ecosystems, in view of devising fishing strategies which prevent the decline of marine populations, such as sardines and anchovies, of paramount importance for countries whose economy is strongly based on fishing activities; (ii) to incorporate stochastic microbial predictive models into a risk assessment process, and therefore to improve the precision of the expected concentrations of a foodborne disease agent. This aspect agrees to the new European approach to food risk assessment and management.

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