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TAKING OVER MARITIME ECOSYSTEMS: MODELLING FISH-JELLYFISH DETERMINISTIC AND RANDOMIZED DYNAMICS

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Abstract. We present the results of a complete phase space analysis for a deterministic two-dimensional predator-prey model representing the key dynamics of fish-jellyfish interactions. Progressing through a series of bifurcations the biological phenomenon of jellyfish blooming is illustrated in this model and thus the taking over of the maritime ecosystem by jellyfish. We then turn to the question of how stochasticity in parameters and equations effects the emerge of blooming. Therefore, we first randomize the essential bifurcation parameter to model/ simulate and discuss stochastic environmental impact and, second, use first principle Markovian birth/ death processes to set-up a system of stochastic differential equations to model/ simulate and discuss the effects of intrinsic noise. In both cases, knowledge about the dynamics of the underlying deterministic system is indispensable and, in particular, in the intrinsic noise case a sooner occurrence of blooming can be observed.

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1 Introduction

The persistence of ecosystems is essential for the survival of food-chains up to global level, especially in situations where human impact exploits and/ or threatens to de-stabilize ecosystems since centuries. Ecosystems and their food-chains are often governed by key predator-prey relationships that keep the ecosystem in a robust balance, like wolves and bison in the Yellowstone national park or fish and jellyfish in maritime ecosystems. Under certain conditions it can happen that the ecosystem balance is disrupted by the prey taking over. This is almost routinely happening during jellyfish blooming, see Refs. [21, 32, 37], such that, e.g., tn the last decade, the aspect of preventing blooms became, beyond ecological reasons, essential for certain coastal regions (especially in Japan).

As outlined in Ref. [39] (see also the literature therein), there are three reasonable causes for jellyfish blooms currently discussed: (I) the competition of jellyfish and fish for food, (II) the influence of water conditions on the predation success of jellyfish and fish, and (III) the predation of young jellyfish by fish.

Jellyfish blooms in terms of the competition for food hypothesis (I) are explained by means of large-amplitude limit cycles based on the well-known Rosenzweig-MacArthur equations, see Ref. [28].

In Ref. [39] we proposed and mathematically analyzed a two-dimensional model for the predation hypothesis (III). This mathematical discussion was later refined and augmented by the study of the funnel phenomenon in Ref. [40]. The funnel phenomenon ensures for almost all initial states that the predator (fish) population gets extinct asymptotically as time tends to infinity whereas the prey (jellyfish) population blooms and continues to proliferate beyond all given bounds. This kind of phenomenon is generated through a sequence of successive (global) bifurcations, starting from an initially asymptotically stable mixed species equilibrium state.

Beyond the deterministic analysis one is interested in the dynamics of ecosystems that are described with the aid of random components. Stochastic effects are added either by inclusion of environmental noise or by inclusion of intrinsic noise that enters the governing equations through first principle Markovian birth and death processes. Once the governing randomized equations are set-up the stability of their solutions is analyzed. A priori, though, it is not clear what stability means in the context of stochastic systems. In particular, if we recall the different convergence notations for sequences of random variables. Besides their ease of applicability it turns out that suitable stochastic stability concepts need to consider all sample paths (almost sure stability), see Ref. [26].

In view of stochastic extensions of our two-dimensional model for the predation hypothesis given in Refs. [39, 40], we present two stochastic versions of this model. The first includes external noise tailored to maritime environments. Specifically, the essential parameter that leads to the key sequence of successive (global) bifurcations is randomized by a Ornstein-Uhlenbeck process leading to a system of random differential equations. We use linearized strong-mean asymptotic stability to discuss the induced blooming behavior of this random system. Second, we present the trail of modeling steps to include intrinsic noise that lead to a Fokker-Planck and from there to an Itô/ Langevin representation of the governing dynamics. The resulting system of stochastic differential equations is then further simplified to illustrate the sooner emerge of the funnel phenomenon under

stochastic effects.

The article focuses on the modeling aspects of the governing equations, and is structured as follows: First, in section 2, we survey the main mathematical results of our two-dimensional deterministic model for the predation hypothesis from Refs. [39, 40]. Next, in section 3, we augment our deterministic model by considering the effect of Ornstein-Uhlenbeck environmental noise. This yields to random ordinary differential equations. Here, we thus additionally provide main results from the theory of random ordinary differential equations with a focus on the concept of linearized strong-mean asymptotic stability. We continue to provide results of a first analysis of the fish-jellyfish model with Ornstein-Uhlenbeck noise and show connections/ differences to the deterministic setting. In section 4, we provide the steps that lead us to a system of stochastic differential equations that includes intrinsic noise into the fish-jellyfish model. Some aspects of the dynamics of this stochastic system with respect to the emerge of jellyfish blooming are then discussed by a suitable linearization together with a simplification of the stochastic diffusion part. Finally, 5 wraps-up the article.

2 A Mathematical Model for Biological Blooming

In Refs. [39, 40] we proposed a two-dimensional model for the mathematical study of the dynamics of a fish-jellyfish ecosystems that experiences a blooming of the jellyfish population and a collapse of the system towards one completely dominated by jellyfish. This predator-prey model for the fish (predator) population x and the jellyfish (prey) population y includes a Holling Type II response, see Refs. [18, 46], and logistic growth constraint for the predatory species while assuming that jellyfish can proliferate even if the carrying capacity for fish is more than surpassed. Our dimensionless model reads

$$\dot{x} \;=\; \left(c + \frac{y}{1+y}\right) x - x^2\,, \qquad \text{and} \qquad \dot{y} \;=\; b\left(1 - d\frac{x}{1+y}\right) y \tag{1}$$

where $c \in \mathbb{R}$ denotes the net birth rate of the fish population (incl. negative rates due to intensive fishing), $b > 0$ stands for the birth and $bd > 0$ for death rate of the jellyfish population, respectively.

For (1) the coordinate axes $x \equiv 0$ and $y \equiv 0$ are invariant such that every solution that starts in the non-negative quadrant $\mathcal{P} := \{(x, y) \in \mathbb{R}_0^+ \times \mathbb{R}_0^+\}$ stays therein for all times. Non-biological negative values for the population sizes cannot occur for solutions starting in $\mathcal{P}$.

Regarding the existing and stability of equilibrium points we showed that only the following three types exist, see Refs. [39, 40]:

Theorem 2.1. [Existence and Stability of Equilibria] **Type 1:** *For all choices of the parameters b, c, d the origin $(x, y) = (0, 0)$ is an unstable extinction equilibrium of the system (1). It is an unstable (hyperbolic) saddle point of for $c < 0$ and a Lyapunov-unstable node for $c > 0$*

Type 2: *For $c > 0$ the point $(x, y) = (c, 0)$ is an additional pure fish population equilibrium in $\mathcal{P}$ that is asymptotically Lyapunov-stable for $d > c^{-1}$ and a saddle point for*

$0 \leq d < c^{-1}$. *In particular, at* $c = 0$ *the equilibrium* $(c, 0)$ *bifurcates from the equilibrium at the origin. This bifurcation is transcritical with respect to the parameter* c.

Type 3: *If the parameter values are such that* $(c+1)^2 - 4d^{-1} \geq 0$ *together with*

$$z_1 \;:=\; \tfrac{1}{2}\left(c + 1 + \sqrt{(c+1)^2 - 4d^{-1}}\right) \;>\; d^{-1}$$

and/ or

$$z_2 \;:=\; \tfrac{1}{2}\left(c + 1 - \sqrt{(c+1)^2 - 4d^{-1}}\right) \;>\; d^{-1}$$

hold, then points $(x, y) = (z_1, dz_1 - 1)$ *and/ or* $(x, y) = (z_2, dz_2 - 1)$ *are mixed species equilibria in* $\mathcal{P}$. *The equilibrium* $(z_1, dz_1 - 1)$ *is always an unstable (hyperbolic) saddle point when it exists. The equilibria* $(z_2, dz_2 - 1)$ *bifurcate from the equilibrium* $(c, 0)$ *for* $0 < c < 1$.

The stability of $(z_2, dz_2 - 1)$ *depends on the critical value* $b^* = -j_2 dz_2 (dz_2 - 1)^{-1}$ *as well as*

$$b_- \;:=\; \tfrac{2 + j_2 dz_2 - 2\sqrt{1 + j_2 dz_2}}{dz_2 - 1} \;>\; 0 \quad \textit{and} \quad b_+ \;:=\; \tfrac{2 + j_2 dz_2 + 2\sqrt{1 + j_2 dz_2}}{dz_2 - 1} \;>\; 0\,.$$

Then, the equilibrium at $(z_2, dz_2 - 1)$ *is hyperbolic and asymptotically Lyapunov-stable for all values of* $0 < b < b^*$. *It is a stable node of the second kind if* $b \in (0, b_-)$, *it is a stable node of the first kind if* $b = b_-$ *and it is a stable focus if* $b \in (b_-, b^*)$. *The equilibrium at* $(z_2, dz_2 - 1)$ *is hyperbolic and unstable in the sense of Lyapunov for all values of* $b > b^*$. *In this case it is an unstable focus if* $b \in (b^*, b_+)$, *it is an unstable node of the first kind if* $b = b_+$ *and it is an unstable node of the second kind if* $b \in (b_+, \infty)$. *The equilibrium at* $(z_2, dz_2 - 1)$ *is non-hyperbolic for* $b = b^*$, *there the matrix of linearization around* $(z_2, dz_2 - 1)$ *has a pair of purely imaginary eigenvalues such that the equilibrium at* $(z_2, dz_2 - 1)$ *undergoes an Andronov-Hopf bifurcation.*

Moreover, roughly speaking (see Ref. [40] for details), if $c \geq 0$ the Andronov-Hopf bifurcation of the equilibrium at $(z_2, dz_2 - 1)$ with increasing values of b is sub-critical and if $c < 0$ then it is super-critical.

A short calculation shows that z_2 is admissible if and only if

$$\begin{aligned}(c, d) \;\in\; \Gamma_2 \;\;:=\;\; & \left\{(c, d) \in (-1, 0] \times \mathbb{R}_0^+ \;:\; 4(1 + c)^{-2} \leq d\right\} \\ & \cup \left\{(c, d) \in (0, 1) \times \mathbb{R}_0^+ \;:\; 4(1 + c)^{-2} \leq d \leq c^{-1}\right\}\,,\end{aligned}$$

and that z_1 is admissible if and only if

$$(c, d) \;\in\; \Gamma_1 \cup \Gamma_2\,, \quad \text{with} \quad \Gamma_1 \;:=\; \left\{(c, d) \in \mathbb{R}^+ \times \mathbb{R}_0^+ \;:\; c^{-1} < d\right\}\,.$$

(Note, for $4(1 + c)^{-2} = d$, we have that $z_1 = z_2$ coalesce giving raise to a saddle-node bifurcation.) Hence, except of the origin, system (1) can have at most three additional equilibria depending on the parameters c and d. Evidently, the existence of equilibria is independent of the jellyfish's birth factor b.

The dynamics of the fish-jellyfish system (1) are sketched in figure 1. The essential part is the existence of blooming areas (BA) that yield, in a funnel like phenomenon, to the unbounded increase (with increasing values of b) of the jellyfish population from the previously asymptotically stable mixed spices equilibrium at $(z_2, dz_2 - 1)$, see Ref. [40].

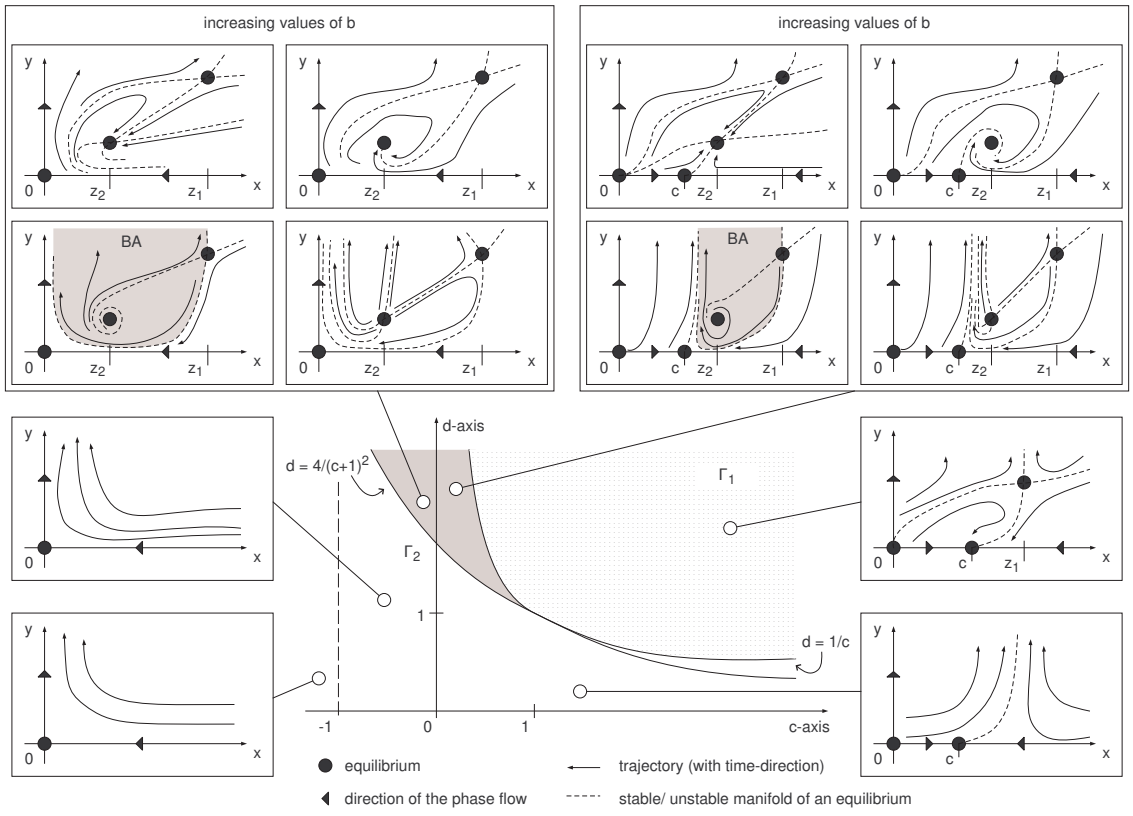

Figure 1: Sketch of the regions Γ_1 (light gray) and Γ_2 (shaded) in the (c, d)-parameter plane together with illustrations of the location of the equilibria for representative choices of c and d, as well as of corresponding invariant manifolds (dashed curves) and selected orbits for increasing values of b. The shadowed regions of those phase portraits are blooming areas (BA).

Theorem 2.1. [**The Funnel Phenomenon**] *Consider the system governed by the equations in (1), assume that the values of the parameters c and d are contained in the interior of* Γ_2*, and let b be sufficiently large. Then, for almost all initial states in* $\mathcal{P}$*, the predator (fish) population gets extinguished asymptotically as time tends to infinity. This kind of phenomenon is generated through a sequence of successive (global) bifurcations as b increases, starting from an asymptotically stable mixed species equilibrium state.*

To establish the funnel behavior of the strongly unstable manifold of $(z_2, dz_2 - 1)$ for b sufficiently large, we rescale the time variable in (1) by setting $\tau = bt$ to derive the equivalent system

$$x' \;=\; \frac{1}{b}\left(c + \frac{y}{1+y} - x\right)x\,, \quad \text{and} \quad y' \;=\; \left(1 - d\frac{x}{1+y}\right)y\,,$$

and in the limit, as $b \to \infty$, the system

$$x' \;=\; 0\,, \quad \text{and} \quad y' \;=\; \left(1 - d\frac{x}{1+y}\right)y\,.$$

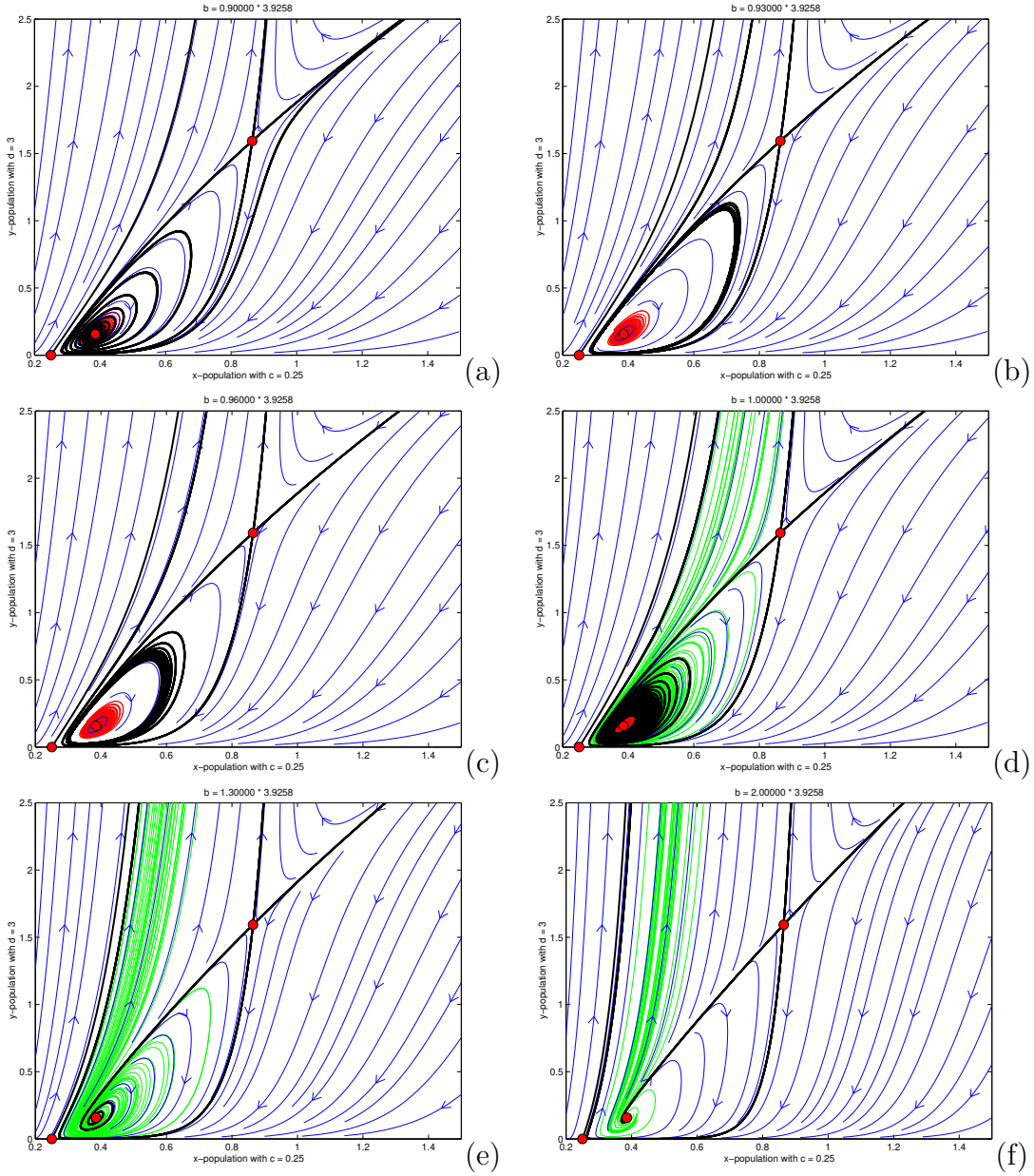

Figure 2: Numerical simulation for the occurrence of a blooming area in the phase space after a sub-critical Andronov-Hopf-bifurcation.

Figure 2 illustrates some results of numerical simulations of the dynamics in the x-y-plane for $c = 0.25$, $d = 3$ and increasing values of b through the critical value $b^* \approx 2.8431$. Here, the red color is used to indicate trajectories that stay within a bounded region of phase space; those trajectories that eventually tend to infinity are displayed in green color. Black lines represent invariant manifolds of the equilibria.

3 Extension of the Model by Environmental Noise

Next, we argue that Ornstein-Uhlenbeck noise is an appropriate noise for including randomness in maritime ecosystems such that we set-up a corresponding random ordinary differential equation model as an extension of (1). Moreover, in this section, we provide some results from the theory of random ordinary differential equations that connect these noisy equations in a path-wise sense to ordinary differential equations. Note, this interpretation is a distinguishing factor of this type of equations from stochastic ordinary differential equations, as the later require an interpretation of the corresponding stochastic integrals in the sense of Itô or Stratonovich. Finally, we discuss the pre-steps of blooming in the previously derived random model.

3.1 Inclusion of Environmental Noise

The easiest way to introduce noise to a system is given by randomizing certain coefficient functions b_i under the assumption of a varying environmental influence on these functions. This leads, for instance, to

$$b_i \;\mapsto\; b_i \,+\, \sigma(b_i)\cdot\xi_t\,,$$

where ξ_t stands for some appropriately chosen noise and $\sigma(b_i)$ is the noise intensity. Though, one has to be careful with this approach when randomizing strictly positive coefficients as the introduction of $\sigma(b_i)\xi_t$ leads to negative values of the resulting process as well. For instance, Ref. [24], pp. 253, addresses this issue and gives hints on how to work around it by setting up primary equations with coefficients in $\mathbb{R}$ instead of $\mathbb{R}^+$.

Following Refs. [31, 43] it is reasonable to assume that many instances of noise occurring in nature behave such that their frequencies f scale according to an inverse power law $f^{-\beta}$. In this setting, white noise is a special case with $\beta = 0$ where all frequencies contribute equally to the power spectrum, while colored noises are dominated by frequencies in a certain range. Specifically, red/ pink noise ($\beta = 1$) is dominated by low frequency (or long-period) cycles and the underlying stochastic process has auto-correlated increments. In the time domain, this produces an increased probability of having long runs of above (or below) average conditions; more intense slopes have been termed brown ($\beta = 2$). Recently, Ref. [47] investigated 152 (temperature) data sets of maritime, coastal and inland terrestrial environments to consolidate this hypothesis: it was shown, that noise in terrestrial environments tends to be white ($\beta < 0.5$)[1], whereas noise in maritime environments (coastal and sea surface) tend to be red/ pink ($\beta \approx 1$) or brown ($\beta \approx 2$)[2].

The importance of colored noise for biological systems in general becomes immediate when recalling Refs. [36, 38, 44], who showed that population persistence and extinction are influenced by noise color; though the effect of noise may be masked by periodic or chaotic dynamics, see Ref. [35]. Moreover, Ref. [27] predicted an increased risk of extinction in populations experiencing red/ pink noise relative to those experiencing white noise, based upon the simple observation that in red/ pink noise long runs of "poor"

[1] Analyzing lakes and rivers, Ref. [14] found white or at most pink $\beta \approx 0.5$ spectra, which suggests that these systems are strongly coupled to the terrestrial environment.

[2] See, Ref. [13], p. 970, for a summary geophysical data showing the range of spectral exponents β found in nature.

conditions for survival are more likely than they are in white noise[3]. Ref. [13] shows that very long population persistence times are more likely for black noise ($\beta = 3$) than for red/ pink one.

A typical brown noise is the **standard Ornstein-Uhlenbeck process** $\xi_t \sim \mathcal{N}(0, \frac{1}{2}(1-\mathrm{e}^{-2t}))$, a Gaussian process that satisfies the stochastic ordinary differential equation

$$\mathrm{d}\xi_t \;=\; -\xi_t \mathrm{d}t + \mathrm{d}W_t\,, \qquad \xi_0 \;=\; 0 \tag{2}$$

with $\mathrm{d}W_t$ denoting (Gaussian) white noise derived from the standard Wiener process $W_t \sim \mathcal{N}(0,t)$. The Ornstein-Uhlenbeck process is a stationary process (all finite dimensional distributions are invariant under time translation), and the Fourier transform of the auto-correlation of its stationary distribution reads as, see Ref. [48],

$$S(f) \;=\; \frac{1}{1+4\pi^2 f^2}$$

and shows the brown noise f^{-2} frequency power law spectrum[4]. Contrary to stochastic integrals with respect to the Wiener process, integrals with respect to the Ornstein-Uhlenbeck process ξ_t are defined in the sense of Riemann integrals as the increments of ξ_t are of bounded variation. Moreover, ξ_t is an ergodic process (i.e. mathematical and sample path mean are identical).

In the following, we consider, as usual in random dynamical systems, ξ_t as a stochastic process with two-sided time, i.e. defined on $\mathbb{R}$.

3.2 The Blooming Model with Ornstein-Uhlenbeck Noise

We have seen in section 2 that the parameter b associated to the jellyfish birth rate is the determining factor for the Andronov-Hopf bifurcation of the mixed species equilibrium at $(z_2, dz_2 - 1)$ that then gives rise to the blooming activity. In view of environmental maritime conditions that may slightly impact the birth rate randomly (temperature fluctuations, availability of food, security of seabed areas for juvenile jellyfish, etc.), we assume a randomization of this parameter as

$$b \;\mapsto\; b + \tfrac{1}{N_e}\xi_t\,,$$

where ξ_t is the Ornstein-Uhlenbeck process according to (2) and N_e is some natural effective population size that scales the effect of the noise (see Refs. [15, 17] for this scaling approach). Thus, our deterministic system (1) becomes the following system of coupled random ordinary differential equations

$$\dot{x}_t \;=\; \left(c + \frac{y_t}{1+y_t}\right) x_t - x_t^2\,, \tag{3}$$

$$\dot{y}_t \;=\; b\left(1 - d\frac{x}{1+y_t}\right) y_t + \tfrac{1}{N_e}\left(1 - d\frac{x}{1+y_t}\right) y_t \xi_t\,. \tag{4}$$

[3]See Ref. [47] for further literature sources supporting this hypothesis.

[4]Concerning applications of the Ornstein-Uhlenbeck process, for instance, Ref. [30] discusses a general version of the Ornstein-Uhlenbeck process with respect to Bacteria growth by considering the simple 1-dimensional logistic growth model of the form $\dot{x}_t = (a + \xi_t)x_t - bx_t^2$.

The subscript 't' at x_t and y_t indicates that we view x_t and y_t as stochastic processes. Here, we have that the equilibria of the deterministic system are preserved and, due to the path-wise nature of the solutions, the non-negative quadrant $\mathcal{P}$ stays invariant (see Refs. [11, 12] for a general invariance result based on path-wise solutions).

Before we continue, let us provide some background on random ordinary differential equations and stability of their equilibria.

3.3 Some Results from the Theory of Random Ordinary Differential Equations

Random ordinary differential equations are less commonly studied compared to white-noise driven stochastic ordinary differential equations, we therefore briefly sketch some essential notions and results that allow us to mathematically analyze the blooming model with Ornstein-Uhlenbeck noise. For simplicity, these notions and results are framed with respect to deterministic initial conditions. For general descriptions and proofs we refer to the literature, e.g. Refs. [8, 41].

Let $X_t : \Omega \times I \to \mathbb{R}^d$ be a stochastic process, $t_0 \in I$ and $x_0 \in \mathbb{R}^d$. Then X_t is called **path-wise solution** on I with respect to the (deterministic) initial condition $(x_0, t_0) \in \mathbb{R}^d \times I$ of the initial value problem for the random ordinary differential equation (RODE)

$$\frac{\mathrm{d}X_t}{\mathrm{d}t} \;=\; \dot{X}_t \;=\; f\left(X_t, t, \omega\right), \qquad X_{t_0} \;=\; x_0\,, \tag{5}$$

if almost all paths $X_{t,\omega}$ of X_t on I obey the (deterministic) ordinary differential equation

$$\frac{\mathrm{d}X_{t,\omega}}{\mathrm{d}t} \;=\; \dot{X}_{t,\omega} \;=\; f\left(X_{t,\omega}, t, \omega\right), \qquad X_{t_0,\omega} \;=\; x_0\,, \tag{6}$$

i.e. the equivalent integral representation

$$X_{t,\omega} \;=\; x_0 + \int_{t_0}^{t} f\left(X_{\tau,\omega}, \tau, \omega\right) \mathrm{d}\tau$$

is well-defined. As we have already seen, this is the case for integrals with respect to the Ornstein-Uhlenbeck process.

Let X_ω and Y_ω be two random variables from Ω to $\mathbb{R}^d$, and X_t and Y_t be two stochastic processes from $\Omega \times I$ to $\mathbb{R}^d$. If the identity $X_\omega = Y_\omega$ holds for almost all $\omega \in \Omega$ we use the notation $X \hat{=} Y$. If $X_t \hat{=} Y_t$, for all $t \in I$, i.e. X_t and Y_t are equivalent, then sets $\Omega_t \in \mathcal{A}$, $t \in I$, exists with $\mathbb{P}(\Omega_t) = 1$ such that $X_{t,\omega} = Y_{t,\omega}$ for $(t, \omega) \in \cup_{t \in I} \left(\{t\} \times \Omega_t\right)$. We use the notation $X_t \overset{I}{=} Y_t$ if theses sets Ω_t can be chosen independently of t, i.e. $\Omega_t \equiv \Omega^*$ for all $t \in I$, and it thus holds that $X_{t,\omega} = Y_{t,\omega}$ for all $(t, \omega) \in I \times \Omega^*$.

The path-wise solution of the RODE (5) is called **unique** on I, if

$$X_t \;\overset{I}{=}\; Y_t$$

holds for each arbitrary pair X_t, Y_t of path-wise solutions for this initial condition.

Theorem 3.1. [Existence and Uniqueness] *Let us consider the RODE* (5) *and assume that the following conditions are satisfied for the right-hand side function* $f(x,t,\omega)$*:*

1. *it is* $\mathcal{A}$*-measurable for all* $(x,t) \in \mathbb{R}^d \times I$*, and continuous on* $\mathbb{R}^d \times I$ *for almost all* $\omega \in \Omega$*, as well as*
2. *for almost all* $\omega \in \Omega$ *there is a real continuous function* $L(t,\omega)$ *on* I *such that*

$$\|f(x_1,t,\omega) - f(x_2,t,\omega)\| \;\leq\; L(t,\omega) \cdot \|x_1 - x_2\|$$

holds at $t \in I$ *and* $x_1, x_2 \in \mathbb{R}^d$*.*

Then, for any initial condition $(x_0,t_0) \in \mathbb{R}^d \times I$ *there is a unique path-wise solution of this RODE on* I*.*

The study of stability concepts for stochastic systems started with Andronov's, Pontrajagin and Vitt's work 'On a statistical study of dynamic systems' (see Ref. [5]), where two-dimensional non-linear systems subject to Gaussian white noise are treated. There, the Fokker-Planck equation for such systems is set-up and the system's asymptotic behavior for $t \to \infty$ is considered applying both Lyapunov's method as well as Kolmogorow's results on Markov- and diffusion processes, see Ref. [23]. First studies of stability analysis of stochastic systems focused on the stability of the first and second moments despite that in applications trajectories are observed instead of moments, see Refs. [9, 29, 42]. In particular Ref. [26] highlights the importance of considering (almost) all trajectories within the stability concepts, i.e. the use of almost sure stability. As examples have shown that there are almost surely stable stochastic systems whose rth moments are unbounded for all $r \geq 1$ and others which are stable in the first moment but unstable in the second moment. Though, the discussion of almost sure stability may be extremely cumbersome such that a vast variety of different stability concepts have survived, see Refs. [8, 23, 26]. Further important highlights in the study of stochastic stability include Oseledets' Multiplicative Ergodic Theorem, see Ref. [33], i.e. a generalization of the Theorem of Hartman and Grobman to connect linear and non-linear stability, the notion of Random Dynamical Systems, see Ref. [7], with its cocycle property for path-wise solutions as a generalization of the flow property present in deterministic dynamical systems, and the notion of pull-back attraction and stability, see Ref. [10].

Here, we use the concept of linearized strong-mean asymptotic stability that allows a discussion in terms of an averaged setting (mean) by means of (strong) asymptotic convergence of the linearization (which typically is accessible more easily). Without loss of generality, let the constant zero-solution $X_t = 0$ be an equilibrium of the RODE (5), i.e. $f(0,t,\omega) = 0$. Moreover, let $A_t = D_x f(X_t,t,\omega)\,|_{X_t=0}$ be the linearization of $f(X_t,t,\omega)$ at $X_t = 0$. Then, 0 is called a **linearized strong-mean asymptotic stable equilibrium** if for all path-wise solutions X_t of

$$\dot{X}_t \;=\; A_t X_t\,,$$

and sufficiently small $\alpha > 0$ it holds that

$$\lim_{t\to\infty} \mathrm{e}^{\alpha t}\,\|X_t\| \,\hat{=}\, 0\,.$$

A helpful result to establish linearized strong-mean asymptotic stability was given by Kozin in Ref. [25], see Ref. [8], p. 72, or Ref. [41], pp. 465, as well for the proof.

Theorem 3.2. [Exponential Decay of Solutions] *Let*

$$\dot{X}_t \;=\; (A + F_t)\, X_t\,,$$

where A is a constant real $d \times d$-matrix and F_t is a path-wise continuous $d \times d$-matrix process, such that the following conditions are satisfied:

1. *All eigenvalues of A have negative real parts such that $\|\exp(At)\| < \beta \mathrm{e}^{-\alpha t}$, $\alpha, \beta > 0$, holds.*

2. *The matrix F_t is path-wise continuous, stationary and ergodic.*

3. *It holds that $\mathbb{E}(\|F_t\|) \leq \gamma < (\alpha - \varepsilon)/\beta$ with $\varepsilon > 0$ for a constant γ.*

Then,

$$\lim_{t\to\infty} \mathrm{e}^{\varepsilon t}\, \|X_t\| \;\hat{=}\; 0$$

holds for any path-wise solution X_t of $\dot{X}_t = (A + F_t)\, X_t$.

3.4 Mathematical Aspects of the Jellyfish Blooming in the Ornstein-Uhlenbeck Noise Model

Considering the RODE (3)-(4) the introduced noise can either lead to an earlier occurrence of the Andronov-Hopf bifurcation or to stabilizing the asymptotic stable behavior of the mixed-species equilibrium at $(z_2, dz_2 - 1)$ beyond b^*.

Figure 3 illustrates twenty sample paths (generated by the Euler method) with initial conditions $(x_0, y_0) = (0.6, 0.5)$ near $(z_2, dz_2 - 1)$ that indicate exactly this for $c = 0.25$ and $d = 3$. The left-hand column provides the time-evolution of the x-variable both in (3)-(4) (dashed lines) as in the deterministic model (1) (solid line) for increasing values of b. Analogously, the right-hand column provides the information for the y-variable. The time stepping is 10^{-4} and scaling parameter $N_e = 10$ being about an order of magnitude larger that the initial conditions (such that we expect still a rather small impact of the noise, which is, e.g., visible by the still very smooth nature of the random trajectories in the figure). We see the oscillatory behavior of the deterministic solutions about the mixed species equilibrium and their escape with increasing values of b. Though, some of the random paths continue to show this oscillatory behavior for values of b at which the deterministic solutions are clearly no longer attracted to the mixed-species equilibrium.

Hence, when performing an stability analysis that involves (almost) all paths, then we expect a critical value of the random system about the mixed-species equilibrium at $(z_2, dz_2 - 1)$ for asymptotic stability that is less than b^*. Then, with increasing values of b an increased probability of a large enough portion of the paths will not be attracted to this equilibrium until we can for sure say that (almost) all paths escape and the equilibrium at $(z_2, dz_2 - 1)$ is unstable.

To mathematically analyze the mixed-species equilibrium at $(z_2, dz_2 - 1)$ in (3)-(4) in terms of the introduced linearized strong-mean asymptotic stability, we first obtain the corresponding linear system of the governing dynamics about $(z_2, dz_2 - 1)$. Here, we

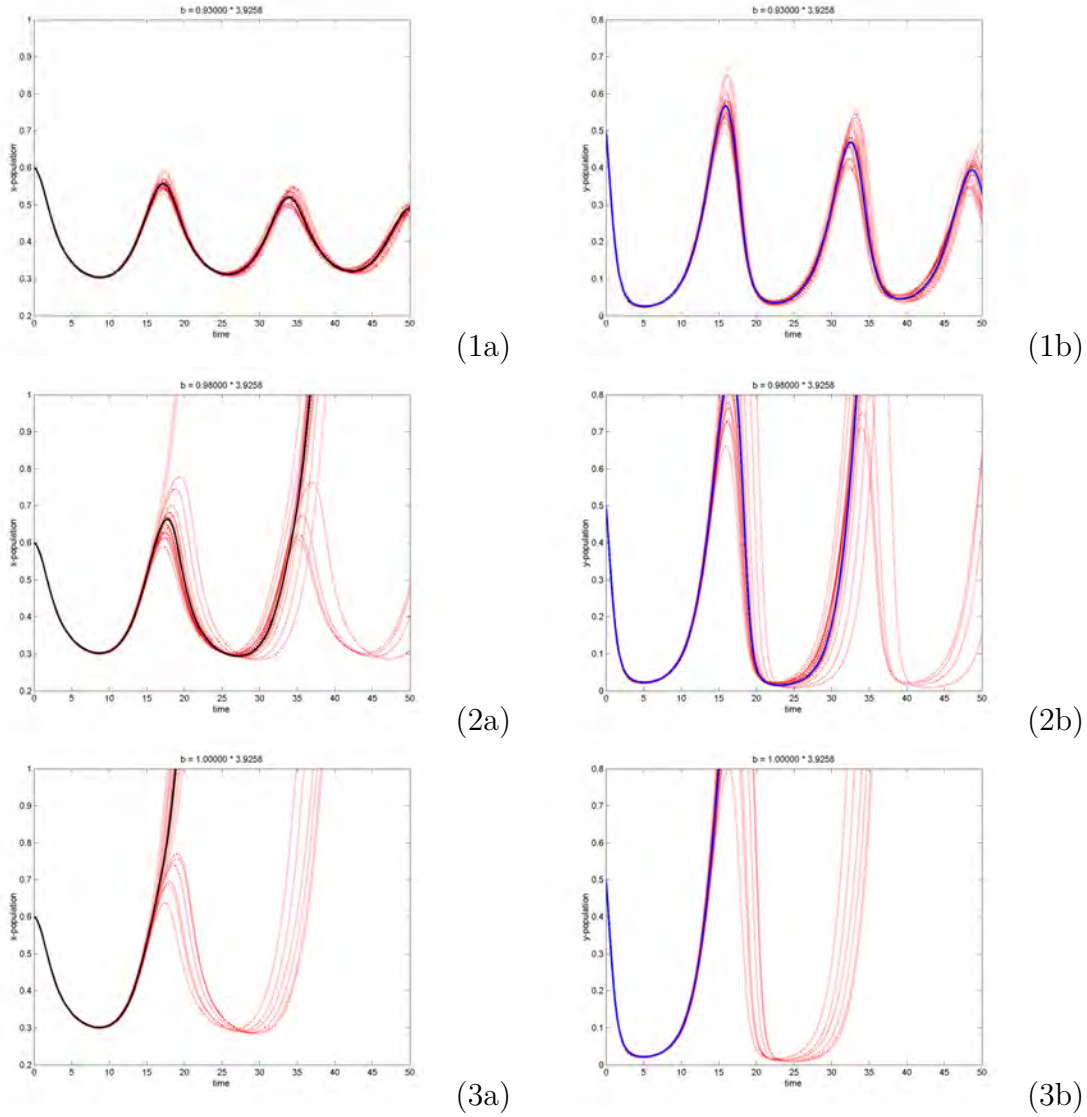

Figure 3: Numerical simulation of the Ornstein-Uhlenbeck noise model for the occurrence of a blooming area in the phase space after a sub-critical Andronov-Hopf-bifurcation.

can reuse the information about the linearization of the deterministic system obtained in Refs. [39, 40], such that the matrix of linearization of (3)-(4) in this case reads

$$A_t \;=\; \begin{pmatrix} j & \frac{1}{d^2 z_2} \\ -(b+\frac{1}{N_e}\xi_t)\cdot d\frac{dz_2-1}{z_2} & (b+\frac{1}{N_e}\xi_t)\cdot\frac{dz_2-1}{dz_2} \end{pmatrix} \quad \text{with} \quad j \;:=\; c+1-2z_2-(dz_2)^{-1}\,.$$

The matrix process

$$A_t \;=\; \underbrace{\begin{pmatrix} j & \frac{1}{d^2 z_2} \\ -bd\frac{dz_2-1}{z_2} & b\frac{dz_2-1}{dz_2} \end{pmatrix}}_{=C_1} + \frac{1}{N_e}\underbrace{\begin{pmatrix} 0 & 0 \\ -bd\frac{dz_2-1}{z_2} & b\frac{dz_2-1}{dz_2} \end{pmatrix}}_{=C_2}\xi_t$$

is a linear transformation of an Ornstein-Uhlenbeck process and thus, stationary, path-

wise continuous, and ergodic. In particular, $F_t = \frac{1}{N_e} C_2 \xi_t$ with $\mathbb{E}(F_t) = 0$, such that the conditions of Theorem 3.2 are satisfied if C_1 has eigenvalues with negative real part, which happens, according to Theorem 2.1, for $b < b^*$.

Note, due to $\mathbb{E}(\xi_t) = 0$, this result is independent of the magnitude $\frac{1}{N_e}$ by which the Ornstein-Uhlenbeck noise enters our governing equations. By decreasing N_e one can easily see in simulations that there are some trajectories displaying unstable behavior for parameters that yield to deterministic stability of the equilibrium. This is certainly one of the drawbacks of including mean-information in the discussion of stability. On the other hand, such a decreasing of N_e may also lead to some stabilization by noise.

In terms of our explanation of jellyfish blooming by instability of the equilibrium at $(z_2, dz_2 - 1)$ Theorem 3.2 is to be interpreted in the sense of a time reversal, i.e. that in the α-limit (for time $t \to -\infty$) the equilibrium is attractive. Hence, linearized strong-mean instability in (3)-(4) is as well governed by the deterministic setting and, in this case, by $b > b^*$.

4 Extension of the Model by Intrinsic Noise

In the following we will use the building blocks of the dimensionless deterministic model (1) to state Markovian birth and death events and to thus derive time and state discrete transitions between states where at most one change in the amount of the number of jellyfish or fish has taken place.

Figure 4 illustrates our further modeling steps (see Refs. [15, 17])[5]. After having derived the time and state discrete transitions between changes in the populations (first principles), we apply the Chapman-Kolmogorow transition equation to obtain a description of the underlying discrete densities. By virtue of a Taylor-expansion with respect to the changes in the states and a continuum limit in the state variables this evolution equation is transformed into a time-difference continuous state evolution. Next, the continuum limit with respect to time leads us to the continuous evolution of the population densities by means of a (approximate) Fokker-Planck equation (density approach). Finally, and not shown in figure 4, the Fokker-Planck equation is transformed into its equivalent Itô/ Langevin stochastic differential equation (trajectory approach).

4.1 Formulation of the Building Blocks

To not get confused with our previous models, we denote the (time-dependent) amounts of (adult) fish by $n_F(t)$ and of jellyfish by $n_J(t)$. As usual the time interval Δt is assumed sufficiently small to enable just one 'birth' or death 'event'.

Based on (1), we assume that the transition probability of one birth event for the fish population occurring during the time interval Δt is one the one hand proportional to the number of existing fish and on the other hand to the amount of resources, i.e. in particular their feeding upon jellyfish. Hence, the transition probability of one birth event reads as a combination as a one point change (just involving n_F) and a two point change

[5]See also Refs. [1, 2, 3, 4] for this stochastic modeling ansatz and its application in mathematical biology.

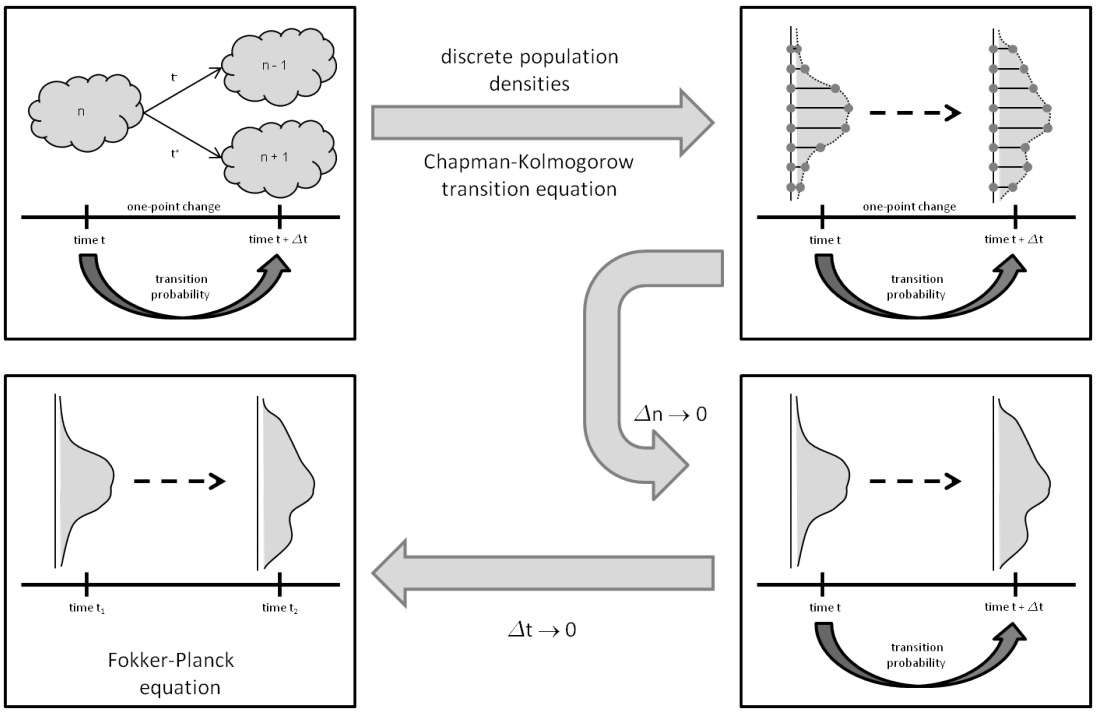

Figure 4: Illustration of the modeling approach that allows us to construct from first principles (i.e. Markovian birth and death processes) the evolution of the population densities by means of a Fokker-Planck equation.

(involving both n_F and n_J)

$$\mathbb{P}\left(n_F+1, n_J, t+\Delta t \,|\, n_F, n_J, t\right) \;=\; \Delta t \cdot \left(c + \frac{n_J}{1+n_J}\right) \cdot n_F + o(\Delta t) \;=:\; t_F^+ \,,$$

where $c > 0$, and $o(\Delta t)$ summarizes terms on a faster time scale, and that the transition probability of one death event is

$$\mathbb{P}\left(n_F-1, n_J, t+\Delta t \,|\, n_F, n_J, t\right) \;=\; \Delta t \cdot n_F^2 + o(\Delta t) \;=:\; t_F^- \,.$$

Analogously, we assume that the transition probability of one birth event for the jellyfish population occurring during the time interval Δt reads as

$$\mathbb{P}\left(n_F, n_J+1, t+\Delta t \,|\, n_F, n_J, t\right) \;=\; \Delta t \cdot b \cdot n_J + o(\Delta t) \;=:\; t_J^+ \,,$$

and that the transition probability of one death event (resulting as falling prey for the fish population) is

$$\mathbb{P}\left(n_F, n_J-1, t+\Delta t \,|\, n_F, n_J, t\right) \;=\; \Delta t \cdot bd \cdot \frac{n_F \cdot n_J}{1+n_J} + o(\Delta t) \;=:\; t_J^- \,.$$

Finally, the transition probability describing the preservation of the status quo is

$$\mathbb{P}\left(n_F, n_J, t+\Delta t \,|\, n_F, n_J, t\right) \;=\; 1 - \left(t_F^+ + t_F^- + t_J^+ + t_J^-\right) \;=:\; t_0 \,.$$

The nature of the birth and death Markov processes already captures the 'usual' model-intrinsic stochastic effects that are due to the variance the stochastic processes have that model the births, deaths and transitions. Especially, model-extrinsic effects like changing environmental conditions, may they be seasonal or connected to extreme events, like unusual increases in water temperatures or sudden bursts in nutrient availability (maybe due to heavy rainfalls that wash-out nearby land territories), have a strong impact on especially smaller populations. These effects, are not included in the governing equations.

4.2 The Approximate Fokker-Planck Equation (Density Description)

Let $n := (n_F, n_J)^T \in \mathbb{N}^2$. The Chapman-Kolmogorov transition equation between two time steps t and $t + \Delta t$ for a discrete population density $p(n,t) : \mathbb{N}^2 \times \mathbb{R} \to \mathbb{R}$ is given by

$$p(n, t + \Delta t) \;=\; \sum_{n'} \mathbb{P}(n, t + \Delta t \,|\, n', t) p(n', t)\,.$$

Denoting the canonical basis vectors in $\mathbb{R}^2$ by $1_1 := (1,0)^T$, and $1_2 := (0,1)^T$, we get:

$$\begin{aligned} p(n, t + \Delta t) \;&=\; t_0(n) \cdot p(n,t) + t_F^+ \cdot p(n - 1_1, t) + t_F^- \cdot p(n + 1_1, t) \\ &\quad + t_J^+ \cdot p(n - 1_2, t) + t_J^- \cdot p(n + 1_2, t)\,. \end{aligned}$$

Following Ref. [15], we come from discrete population sizes n to continuous population sizes x, by introducing the scaling $x = n/N_e$ for some natural effective population scale N_e such that $\mathbb{E}(n_F(t))/N_e = \mathcal{O}(1)$, $\mathbb{E}(n_J(t))/N_e = \mathcal{O}(1)$ and $\mathbb{V}ar(n_F(t))/N_e \leq \mathcal{O}(1)$, $\mathbb{V}ar(n_J(t))/N_e \leq \mathcal{O}(1)$: Let Δx a small scalar positive quantity. For two analytic functions $\alpha, \beta : \mathbb{R}^2 \to \mathbb{R}$ $(i = 1, 2)$ with Hesse-matrices H_a and H_b their expansion in a Taylor-series about $x$leads to

$$\begin{aligned} &(1 - \alpha(x))\beta(x) + \alpha(x + \Delta x 1_i)\beta(x + \Delta x 1_i) \\ &= \beta(x) - \alpha(x)\beta(x) + \big(\alpha(x) + \nabla\alpha(x)^T 1_i \Delta x + \tfrac{1}{2}\Delta x 1_i^T H_\alpha(x) 1_i \Delta x + o(\Delta x^3)\big) \\ &\quad \cdot \big(\beta(x) + \nabla\beta(x)^T 1_i \Delta x + \tfrac{1}{2}\Delta x 1_i^T H_\beta(x) 1_i \Delta x + o(\Delta x^3)\big) \\ &= \beta(x) + \big(\beta(x)\nabla\alpha(x)^T + \alpha(x)\nabla\beta(x)^T\big) 1_i \Delta x \\ &\quad + \tfrac{1}{2}\left(\beta(x) 1_i^T H_\alpha(x) 1_i + 2\nabla\alpha(x)^T 1_i \cdot \nabla\beta(x)^T 1_i + \alpha(x) 1_i^T H_\beta(x) 1_i\right) \Delta x^2 \\ &\quad + o(\Delta x^3) \\ &= \beta(x) + \nabla(\alpha \cdot \beta)(x)^T 1_i \Delta x + \tfrac{1}{2}\Delta x 1_i^T H_{\alpha\cdot\beta}(x) 1_i \Delta x + o(\Delta x^3) \\ &= \beta(x) + \partial_{x_i}(\alpha \cdot \beta)(x)\Delta x + \tfrac{1}{2}\partial_{x_i}\partial_{x_i}(\alpha \cdot \beta)(x)\Delta x^2 + o(\Delta x^3)\,, \end{aligned}$$

and

$$\begin{aligned} &-\alpha(x)\beta(x) + \alpha(x - \Delta x 1_i)\beta(x - \Delta x 1_i) \\ &= -\partial_{x_i}(\alpha \cdot \beta)(x)\Delta x + \tfrac{1}{2}\partial_{x_i}\partial_{x_i}(\alpha \cdot \beta)(x)\Delta x^2 + o(\Delta x^3)\,. \end{aligned}$$

Introducing the continuous population numbers x_F for the fish and x_J for the jellyfish, together with $\Delta x = N_e^{-1}$ leads to the state-continuous, time-discrete model

$$\begin{aligned}\frac{p(x,t+\Delta t)-p(x,t)}{\Delta t} &= -\sum_{j=F,J}\partial_{x_j}\left(V_j(x)\cdot p(x,t)\right)\Delta x \\ &\quad + \tfrac{1}{2N_e}\sum_{j,k=F,J}\partial_{x_j}\partial_{x_k}\left(G_{j,k}(x)p(x,t)\right)\Delta x^2 + o(\Delta x^3)\,,\end{aligned}$$

where for $x := (x_F, x_J)^T$ the vector-valued drift function $V : \mathbb{R}^2 \to \mathbb{R}^2$ is given as

$$V(x) = \begin{pmatrix} \left(c + \frac{x_J}{1+x_J}\right) x_F - x_F^2 \\ b\left(1 - d\frac{x_F}{1+x_J}\right) x_J \end{pmatrix}, \tag{7}$$

and the symmetric diffusion matrix $G : \mathbb{R}^2 \to \mathbb{R}^{2\times 2}$ read as

$$G(x) = \begin{pmatrix} \left(c + \frac{x_J}{1+x_J}\right) x_F + x_F^2 & 0 \\ 0 & b\left(1 + d\frac{x_F}{1+x_J}\right) x_J \end{pmatrix}. \tag{8}$$

Note, that for each fixed x the matrix G has non-negative eigenvalues only, such that we can take its 'square root' later on.

Finally, scaling the time as $\tau = t/N_e = t\Delta x$ and scaling the continuous density distribution as $\rho(x,\tau)\Delta x = p(x,t)$, we get an approximate Fokker-Planck equation representing our population model:

$$\begin{aligned}\partial_\tau \rho(x,\tau) &= -\sum_{j=F,J}\partial_{x_j}\left(V_j(x)\rho(x,\tau)\right) \\ &\quad + \tfrac{1}{2N_e}\sum_{j,k=F,J}\partial_{x_j}\partial_{x_k}\left(G_{j,k}(x)\rho(x,\tau)\right)\,,\end{aligned} \tag{9}$$

with drift-vector V and diffusion matrix G as in (7) and (8), respectively.

4.3 The Stochastic Version in Terms of Itô/ Langevin Equations (Trajectory Description)

There exists an easy translation from the Fokker-Planck (9) to a stochastic differential equation, see Ref. [45], namely

$$\mathrm{d}X_t = V(X_t)\mathrm{d}t + \tfrac{1}{\sqrt{2N_e}}L(X_t)\,\mathrm{d}W_t\,, \quad \text{with} \quad G(x) = L(x)\,\left(L(x)\right)^T\,,$$

where $W_t = (W_t^{(1)}, W_t^{(2)})^T \in \mathbb{R}^2$ is a vector-valued (standard) Wiener process, with independent scalar (standard) Wiener processes $W_t^{(j)}$, $j = 1, 2$, and $V(x)$ and $G(x)$ as specified

in (7) and (8), respectively. Here, the (Langevin) diffusion matrix L immediately reads as

$$L(x) \;=\; \begin{pmatrix} \sqrt{\left(c+\frac{x_J}{1+x_J}\right)x_F + x_F^2} & 0 \\ 0 & \sqrt{b\left(1+d\frac{x_F}{1+x_J}\right)x_J} \end{pmatrix}.$$

Note, L is unique only up to orthogonal transformations.

This technique leads to the following two-dimensional system of coupled Itô stochastic differential equations (Langevin type) for the fish-jellyfish dynamics:

$$\begin{aligned} \mathrm{d}X_F &= \left(\left(c-\frac{X_J}{1+X_J}\right)X_F - X_F^2\right)\mathrm{d}t \\ &\quad + \tfrac{1}{\sqrt{2N_e}}\sqrt{\left(c+\frac{X_J}{1+X_J}\right)X_F + X_F^2}\;\mathrm{d}W_t^{(1)}, \qquad (10) \\ \mathrm{d}X_J &= \left(b\left(1-d\frac{X_F}{1+X_J}\right)X_J\right)\mathrm{d}t \\ &\quad + \tfrac{1}{\sqrt{2N_e}}\sqrt{b\left(1+d\frac{X_F}{1+X_J}\right)X_J}\;\mathrm{d}W_t^{(2)}. \qquad (11) \end{aligned}$$

The notation change from x to X indicates that $X = (X_F, X_J)^T \in \mathbb{R}^2$ is a stochastic process.

The standard (strong) solution theory of stochastic differential equations, see Ref. [16], is not directly applicable in this (as in many other biological contexts) as it assumes a Lipschitz-condition for the drift and diffusion terms that is certainly violated by the roots involved in our diffusion functions. Moreover, standard results for the invariance of the non-negative quadrant, like Refs. [11, 12], require exactly this notion of a (strong) path-wise solution.

Though, due to our (rigorous) mathematical discussion, see Refs. [39, 40], of the underlying deterministic dynamics governed by (1) we know that for the most interesting aspect of the model, the existence of blooming area and the manifestation of the funnel phenomenon, the origin is deterministically repelling, such that we are actually in regimes that justify Lipschitz continuity of the equations right-hand sides and thus allow us to work with (strong) path-wise solutions.

For a discussion of the theory of stochastic ordinary differential equations we refer to Refs. [16, 34] and, especially, for the theory of stochastic stability to Refs. [6, 7, 22].

4.4 Mathematical Aspects of the White Noise Model

Here, as for the RODE system (3)-(4), our knowledge about the deterministic system pays off. If the parameters are such that the origin is unstable with all trajectories are being repelled, i.e. $c > 0$, and we additionally assume that the noise impact in (10)-(11) is sufficiently small, i.e. N_e sufficiently large, then we expect that trajectories starting in some δ-environment of the origin may avoid a smaller ε-environment of it almost surely.

Hence, we expect Lipschitz-continuity for the right-hand sides of (10)-(11) for all relevant trajectories starting nearby the deterministic equilibrium at $(z_2, dz_2 - 1)$ such that pathwise considerations are valid in these cases.

Note, due to the diffusion part $\frac{1}{\sqrt{2N_e}}L(X_t)$ only the origin stays as an equilibrium point in the stochastic system. Nevertheless, we assume that N_e is typically large enough such that it remains interesting to investigate the behavior of stochastic trajectories about the deterministic equilibrium $(z_2, dz_2 - 1)$.

Figure 5 displays the deterministic phase space together with two stochastic trajectories (left-hand column) as well as the norm of the drift vector field $V(X_t)$ for $c = 0.25$, $d = 3$, and $b = 0.8 \cdot b^*$ in part (a), $b = 0.9 \cdot b^*$ in part (b), as well as $b = 0.93 \cdot b^*$ in part (c). In particular, they show the system's equilibria together with the directions of their stable and unstable eigen-spaces, and, starting at $(x, y) = (0.6, 0.5)$ and $(x, y) = (z_2 + 0.02, dz_2 + 0.02)$, two stochastic trajectories of (10)-(11) with $N_e = 10$ and simulated by virtue of the Milstein method. We observe that the deterministic 'speed' $\|V(X_t)\|$ declines and nearly vanishes at the region connecting the deterministic equilibria at the x-axis and the mixed species equilibria, i.e. in particular about the equilibrium $(z_2, dz_2 - 1)$. Here, the stochastic dynamics are then governed by the stochastic diffusion which may drive the trajectory in regions of larger drift values enforcing a sooner escape (in terms of lower b-values) compared to the deterministic setting.

Let us next construct a **simplified model** about the deterministic equilibrium $(z_2, dz_2 - 1)$ to understand the balance between the asymptotic attraction by the drift part and the diffusive impact of the diffusion part that leads to an escape for parameters like $b = 0.9b$ that deterministically still show a healthy fish-jellyfish ecosystem.

From the deterministic dynamics (section 2) we know that, for parameters that lead to deterministic asymptotic stability of the equilibrium $(z_2, dz_2 - 1)$, that the dynamics locally about this equilibrium are such that trajectories starting near the equilibrium stay near the equilibrium and in particular in a bounded region. Assuming that we scale N_e such that the diffusion part is bounded and $\|\frac{1}{\sqrt{2N_e}}L(x)\|$ small enough in this region, we obtain a simplified model of the form

$$\mathrm{d}X_F = \left(\left(c - \frac{X_J}{1 + X_J}\right) X_F - X_F^2\right) \mathrm{d}t + \sigma_1 \mathrm{d}W_t^{(1)}, \tag{12}$$

$$\mathrm{d}X_J = \left(b\left(1 - d\frac{X_F}{1 + X_J}\right) X_J\right) \mathrm{d}t + \sigma_2 \mathrm{d}W_t^{(2)}. \tag{13}$$

Of course, this simplified model has only a limited realm of validity $\mathcal{U}_{\text{val}}$, though still captures the essence of what may happen locally about the deterministic equilibrium $(z_2, dz_2 - 1)$. As previously, we consider the linearization about $(z_2, dz_2 - 1)$ such that (12)-(13) becomes, with $j := c + 1 - 2z_2 - (dz_2)^{-1}$,

$$\begin{pmatrix} \mathrm{d}X_F \\ \mathrm{d}X_J \end{pmatrix} = \begin{pmatrix} j & \frac{1}{d^2 z_2} \\ -b \cdot d\frac{dz_2 - 1}{z_2} & b \cdot \frac{dz_2 - 1}{dz_2} \end{pmatrix} \begin{pmatrix} X_F \\ X_J \end{pmatrix} \mathrm{d}t + \begin{pmatrix} \sigma_1 & 0 \\ 0 & \sigma_2 \end{pmatrix} \begin{pmatrix} \mathrm{d}W_t^{(1)} \\ \mathrm{d}W_t^{(2)} \end{pmatrix}. \tag{14}$$

Note, that the diffusion part of the simplified model (14) is independent of the state variables X_F and X_J such that we can either interpret this system in the sense of Itô

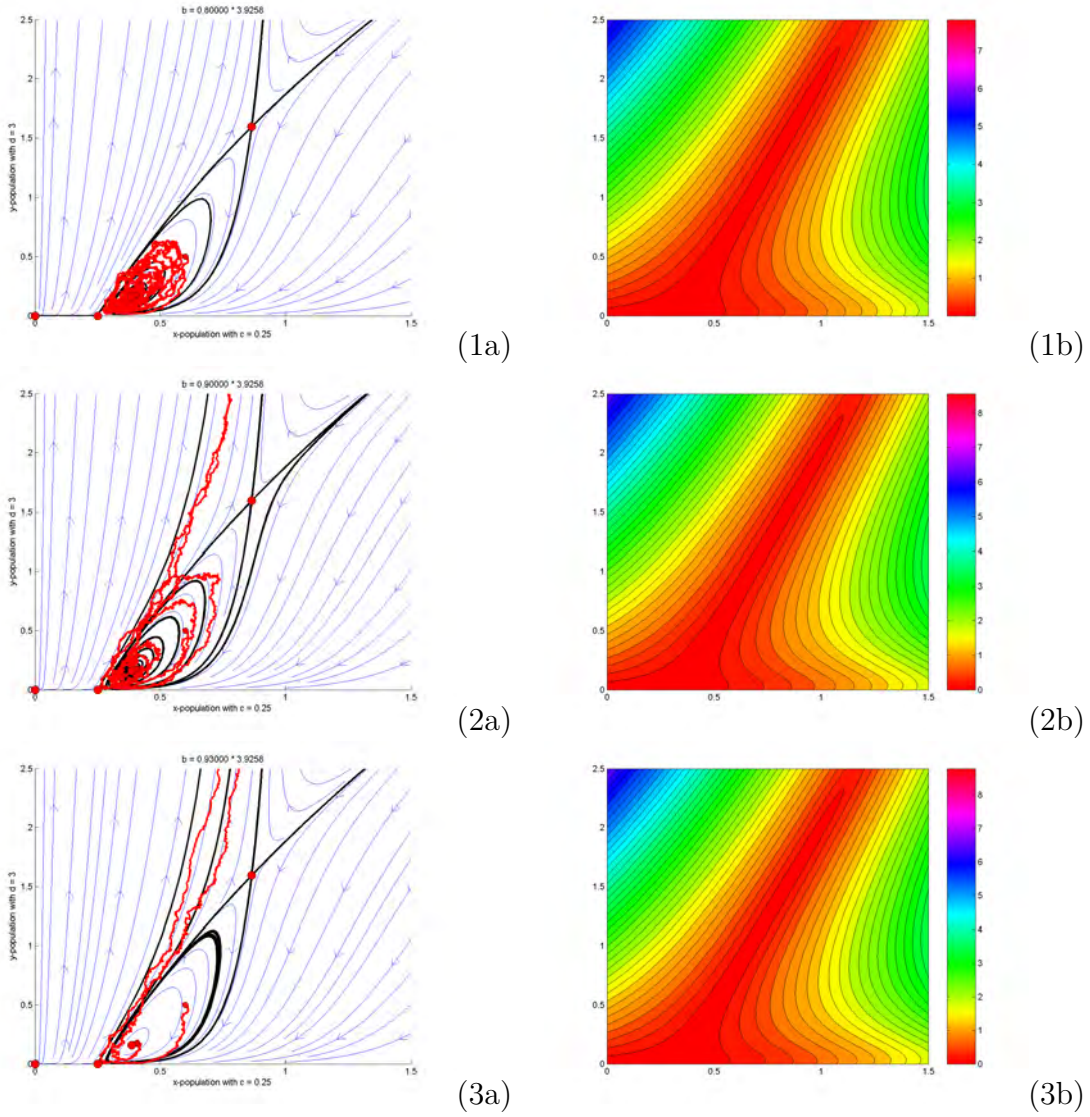

Figure 5: Subfigures in row (a) show the deterministic phase space including two stochastic trajectories (with $N_e = 10$) and row (b) provides the norm of the corresponding deterministic vector-field.

or Stratonovich. Following [19, 20] we introduce the variables Z_F and Z_J such that $X_F = Z_F + \sigma_1 \xi_t^{(1)}$ and $X_J = Z_J + \sigma_2 \xi_t^{(2)}$, respectively, with independent Ornstein-Uhlenbeck processes $\xi_t^{(1)}$ and $\xi_t^{(2)}$. Due to (2) we transform the system of Stratonovich stochastic differential equations (14) into a path-wise equivalent system of random differential equations

$$\underbrace{\begin{pmatrix} \dot{Z}_F \\ \dot{Z}_J \end{pmatrix}}_{=:\dot{Z}_t} = \underbrace{\begin{pmatrix} j & \frac{1}{d^2 z_2} \\ -b \cdot d \frac{dz_2 - 1}{z_2} & b \cdot \frac{dz_2 - 1}{dz_2} \end{pmatrix}}_{=:A} \underbrace{\begin{pmatrix} Z_F \\ Z_J \end{pmatrix}}_{=Z_t} + \underbrace{\begin{pmatrix} \sigma_1 \xi_t^{(1)} \\ \sigma_2 \xi_t^{(2)} \end{pmatrix}}_{=:\Xi_t} . \tag{15}$$

Theorem 4.1. [Boundedness of the Simplified Model] *Let $(z_2, dz_2 - 1)$ be an asymptotically stable equilibrium of the deterministic system (1) such that $\lambda < 0$ is the real part of the largest eigenvalue of A such that $\|e^{At}\| \leq \gamma e^{\lambda}$. Then,*

$$\lim_{t\to\infty} \mathbb{E}(\|Z_t\|) \overset{I}{\leq} -\gamma\lambda^{-1}\sqrt{\tfrac{1}{2}\sigma_1^2 + \tfrac{1}{2}\sigma_2^2}$$

for the solutions Z_t of simplified model (14).

Proof. We assume that our solutions start at $t_0 = 0$ with deterministic initial conditions Z_0 and $\Xi_0 = 0$. Path-wise, (15), is an ordinary differential equations such that we can apply the usual solution formulas[6] to obtain

$$Z_t \overset{I}{=} e^{At} Z_0 + \int_0^t e^{A(t-\tau)}\, \Xi_\tau \, d\tau \,.$$

Let λ be the real part of the largest eigenvalue of A such that $\|e^{At}\| \leq \gamma e^{\lambda}$, then an upper bound of for the solution is obtained as

$$\|Z_t\| \overset{I}{\leq} \gamma\|Z_0\|e^{\lambda t} + \gamma e^{\lambda t} \int_0^t e^{-\lambda\tau}\, \|\Xi_t\|\, d\tau \,,$$

and with $\mathbb{E}\left(\|\Xi_t\|\right) = \sqrt{\sigma_1^2 \mathbb{V}ar(\xi_t^{(1)}) + \sigma_2^2 \mathbb{V}ar(\xi_t^{(2)})} < \sqrt{\frac{1}{2}\sigma_1^2 + \frac{1}{2}\sigma_2^2} \cdot (1 + e^{-t})$, we further receive

$$\begin{aligned}
\mathbb{E}(\|Z_t\|) &\overset{I}{\leq} \gamma\|Z_0\|e^{\lambda t} + \gamma\sqrt{\tfrac{1}{2}\sigma_1^2 + \tfrac{1}{2}\sigma_2^2}\, e^{\lambda t}\left[-\tfrac{1}{\lambda}e^{-\lambda t} - \tfrac{1}{\lambda+1}e^{-(\lambda+1)t}\right]_0^t \\
&= \gamma\|Z_0\|e^{\lambda t} + \gamma\sqrt{\tfrac{1}{2}\sigma_1^2 + \tfrac{1}{2}\sigma_2^2}\left(\tfrac{2\lambda+1}{\lambda(\lambda+1)}e^{\lambda t} - \tfrac{1}{\lambda+1}e^{-t} - \tfrac{1}{\lambda}\right) .
\end{aligned}$$

Hence, as under the assumption of asymptotic stability for which we constructed the simplified model, we have $\lambda < 0$ and thus

$$\lim_{t\to\infty} \mathbb{E}(\|Z_t\|) \overset{I}{\leq} -\gamma\lambda^{-1}\sqrt{\tfrac{1}{2}\sigma_1^2 + \tfrac{1}{2}\sigma_2^2}\,.$$

□

In view of the theorem and several simulation runs shown in figure 6, we expect the solutions of the simplified model to stay in a region $\mathcal{R}$ that is given by a relation that takes the attractive impact due to the value of the (negative) real part λ of the largest eigenvalue into account as well as the diffusive impact resulting from the diffusion parameters σ_1 and σ_2. The larger $|\lambda|$ is the smaller $\mathcal{R}$ stays, and for values of λ approaching zero the expected extension of $\mathcal{R}$ becomes larger. Moreover, for values of λ approaching zero the region $\mathcal{U}_{\text{val}}$ for which the simplified model is satisfied becomes smaller (due to the deterministic bifurcation taking place). Both effects combined[7] illustrate the sooner escape (in terms of lower b-values) compared to the deterministic setting that we observed in the simulations.

[6] Which we could apply for Stratonovich stochastic differential equations immediate as well, or by utilization of Itô's formula for Itô stochastic differential equations, which would yield a bit more notational work.

[7] Of course, just an upper bound for the norm of a solution is not enough to claim that $\mathcal{R}$ is tight in the sense, that $\lim_{t\to\infty} \mathbb{E}(\|Z_t\|)$ may not be in a substantially smaller region.

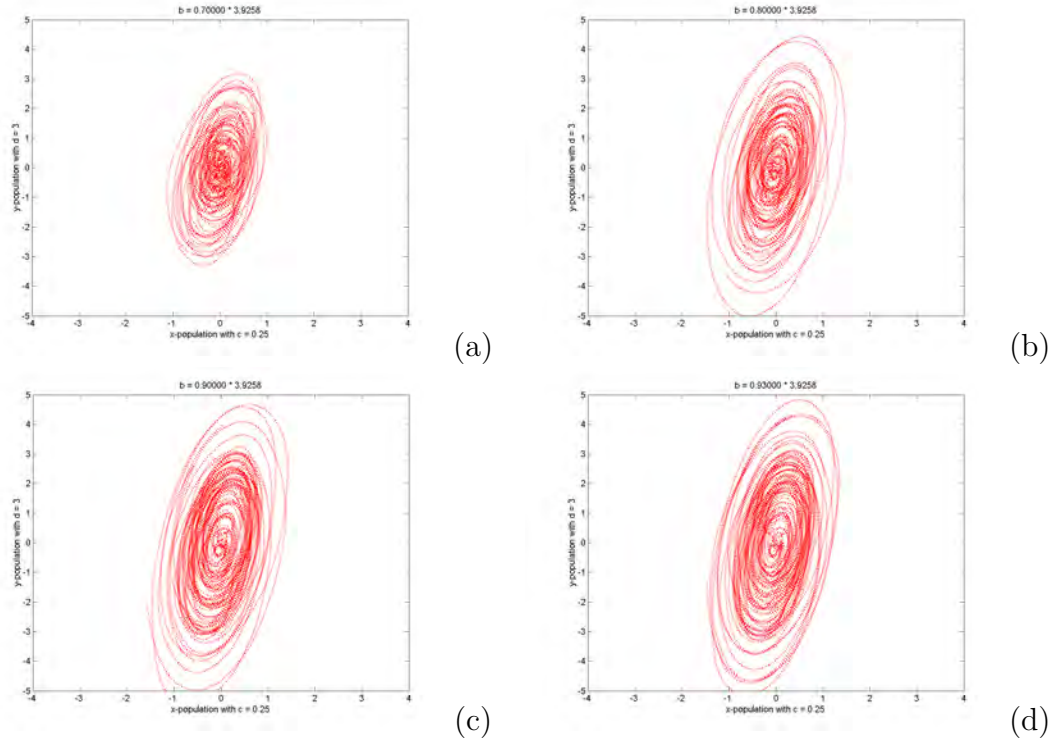

Figure 6: Numerical simulation of the simplified model (14) for increasing values of b from (a) to (b). In each simulation 10 runs are shown each with $\sigma_1 = \sigma_2 = 0.2$

5 Summary and Outlook

We presented a deterministic model for the interaction of fish and jellyfish in a maritime ecosystem, see [39, 40], and extended that to two stochastic systems by first randomizing the essential bifurcation parameter b (leading to a random ordinary differential equation model) and second by utilizing first principle Markovian birth/ death processes to set-up, after several intermediate steps and continuum limits, a stochastic differential equation model. For the first mathematical illustrations of the blooming phenomenon in these stochastic models we played the systems back to linear random ordinary equations that allow, path-wise, a treatment similar to ordinary differential equations.

A common theme in our discussion was the information we obtained from the deterministic dynamics of our predator-prey model system both as input for theoretical discussions (like the existence of path-wise solutions) as well as the driver for the global stochastic dynamics beyond the vicinity of the deterministic equilibrium (vanishing of the drift part). Especially, tailored simplified models can be used about points of interest (with near vanishing drift) in the stochastic phase space and discuss the local dynamics and how that carries solutions to the 'currents' of strong drift.

Our mathematical discussions of the derived stochastic models served as illustrations of the effects observed in the simulations and as first steps towards a rigors understanding of the emergence of the funnel phenomenon in these stochastic systems. In that respect, there remains still work that may have to include concepts of stability that incorporate probability (rather than means) or hitting times to see when certain environments are left

or re-entered.

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