Stochastic Bifurcations in the Plankton-fish System∗

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Since each creature interacts with each other through a food chain, an analysis of the food chain is a crucial problem in an ecosystem. In this paper, we consider the plankton-fish system consisting of fish, zooplankton and phytoplankton, and study the influence of the random noise on the stability of the plankton system under fish school by numerical simulations. The qualitative change of the solutions of differential equations by variation of a system parameter is generally called a bifurcation. This paper is concerned with the bifurcation analysis of a stochastic plankton-fish system. As major analytical methods for the stochastic bifurcation, the D-bifurcation (Dynamical bifurcation) and the P-bifurcation (Phenomenological bifurcation) approaches are cited. The D-bifurcation considers the stability of invariant measures, while the P-bifurcation is characterized with a qualitative change of the stationary probability distribution, e.g., a transition from unimodal to bimodal distribution. By the numerical simulations, we show that not the D-bifurcation but the P-bifurcation occurs in the stochastic plankton-fish system considered here.

1. Introduction

The food chain is a fundamental and an important biological interaction in every living thing, so that the stability analysis of the food chain is one of the major problems in ecosystem [1, 2]. Hence, we consider the stability analysis of the food chain. Environmental changes in the food chain cause some kinds of random fluctuations in the growth and the death rates of species. In order to study the impact of these uncertainties on the food chain, we need the stochastic model. Focusing on the food chain in the ocean or the lake, we propose the stochastic plankton-fish model.

In some cases, we encounter the situation that the stability of the system changes by variation of a system parameter. Such a qualitative change of the system is generally called a bifurcation. In this paper, we analyze the bifurcation in a stochastic plankton-fish system.

In Section 2, we begin with the explanation of the conventional deterministic plankton-fish model [3-5], and propose the stochastic plankton-fish model. Since the behavior of plankton in the stochastic plankton-fish model has a strong relation to the stability of the steady state of the corresponding deterministic model, we study the stability of the deterministic steady state in Section 3. In order to study the bifurcation in the stochastic system, we need the stochastic bifurcation theory [6-11]. Section 4 is devoted to the explanation of the stochastic bifurcation theory. In the stochastic bifurcation theory, there are two types of approaches. One is the D-bifurcation (dynamical bifurcation) approach associated with the stability of invariant measures. The other is the P-bifurcation (phenomenological bifurcation) approach that studies a qualitative changes of the stationary measure corresponding to one-point motion. The D-bifurcation considers the stability of invariant measures, which is related to the study the change of sign of the Lyapunov exponents. In the D-bifurcation approach, the random dynamical system [6], the invariant measure, the random attractor and the multiplicative ergodic theory [6-11] play a central role. Hence, in Section 4, these concepts are summarized. Next, the P-bifurcation is introduced. A major point of the P-bifurcation approach is to study the change of the shape of the stationary solution of the Fokker-Planck equation, for example, change from unimodal to bimodal or crater-like shape.

By using the D- and the P- bifurcations introduced in Section 4, we analyze the influence of the random noise on the bifurcation in the stochastic plankton-fish model by simulations in Section 5. Finally, we
summarize the results obtained in this paper in Section 6, and show that not the D-bifurcation but the P-bifurcation occurs in the stochastic plankton-fish system considered here.

2. Stochastic Plankton-fish System

Letting $u(t), v(t)$ and $f(t)$ be the densities of phytoplankton, zooplankton and fish at time $t \in \Theta \equiv (0,T)$, respectively, the conventional plankton-fish model is given below [2,3]:

$$\frac{du(t)}{dt} = au(t)(1-u(t)) - \frac{u(t)v(t)}{h+u(t)}, \tag{1}$$
$$\frac{dv(t)}{dt} = b\frac{u(t)v(t)}{h+u(t)} - mv(t) - f(t)\frac{nv(t)^2}{n^2 + v(t)^2}, \tag{2}$$

where all constants in (1) and (2) are positive, especially, $h$, $b$ and $m$ denote the half saturation constant, the food conversion and the natural death rates of zooplankton. The 2nd and the 3rd terms of the R.H.S. of (1) and (2) mean the predation rate of zooplankton and fish, which are called the Holling types II and III predation rates [1] respectively. The curves of types II and III differ in that the former is concave, while the latter has an inflection point.

We impose the following initial conditions:

$$u(0) = u_0, \quad v(0) = v_0. \tag{3}$$

In this section, we propose the stochastic plankton-fish model so as to study the influence of the random noise caused by the environmental changes on the behavior of each plankton. Since the phytoplankton and the zooplankton live at the same place or the area in the lake or the sea, the environment around them is thought of as the same condition. Hence, we consider the same environmental fluctuation for the both plankton. By modeling such a random fluctuation by the Gaussian white noise, we derive the stochastic plankton-fish model:

$$du(t) = \left( au(t)(1-u(t)) - \frac{u(t)v(t)}{h+u(t)} \right) dt + \alpha u(t)dW(t), \tag{4}$$
$$dv(t) = \left( b\frac{u(t)v(t)}{h+u(t)} - mv(t) - f(t)\frac{nv(t)^2}{n^2 + v(t)^2} \right) dt + \beta v(t)dW(t), \tag{5}$$

where $\alpha$ and $\beta$ are constants, and $w(t)$ is a standard Wiener process.

3. Stability Analysis

The behavior of the solution of the stochastic plankton-fish model (4) and (5) is closely related to the stability of the steady state of the following deterministic system with the constant fish density $f(t) = f$:

$$\frac{dv(t)}{dt} = b\frac{u(t)v(t)}{h+u(t)} - mv(t) - f\frac{nv(t)^2}{n^2 + v(t)^2}. \tag{7}$$

It is easily shown that (6) and (7) have three steady states $(\bar{u}, \bar{v})$ such that

$$(\bar{u}, \bar{v}) = (0, 0), \quad (1, 0), \quad (u_c, v_c), \tag{8}$$

where $(u_c, v_c)$ is a coexistent steady state defined by the nonnegative solution of

$$v = a(1-u)(h+u), \quad f\frac{nv}{n^2 + v^2} = b\frac{u}{h+u} - m. \tag{9}$$

The dependency of the coexistent steady state $(u_c, v_c)$ on the fish density $f$ is shown in Fig. 1. In Fig. 1, parameter values are set as $a = 5.0, b = 1.0, h = 0.2, m = 0.6, n = 0.4$. As shown in Fig. 1, at the high fish density, phytoplankton-dominated state is the steady state.

![Fig. 1 Dependence of the coexistent steady state on the fish density $f$ ($a = 5.0, b = 1.0, h = 0.2, m = 0.6, n = 0.4$)](image)

As lowering $f$, two steady states appear by the saddle-node bifurcation [12-15] at the point of the filled star in Fig. 1, so that the system becomes bistable. Further lowering $f$, the two steady states disappear by the saddle-node bifurcation at the point of the empty star and the system goes back to the single steady state. At the point indicated by the filled rectangle in Fig. 1, the Hopf bifurcation [12-15] occurs. On the left-side region of the Hopf bifurcation point, a stable limit cycle is observed. The coexistent steady state undergoes the backward supercritical Hopf bifurcation.

4. Stochastic Bifurcations

As the powerful analytical method for the stochastic bifurcation, the D-bifurcation and the P-bifurcation methods are cited [6]. The D-bifurcation approach is
based on the stability of invariant measures, while the P-bifurcation studies a stationary measure corresponding to the one-point motion.

### 4.1 The D-bifurcation

In this section, we explain the basic concepts required for the D-bifurcation.

Let $\Omega$ be a space of continuous functions $\omega: R \rightarrow R$ which satisfy $\omega(0) = 0$, i.e.,

$$\Omega = \{\omega \in C(R) | \omega(0) = 0\}. \quad (10)$$

And let $(\Omega, \mathcal{F}, P)$ be a probability space and $\{\theta_t: \Omega \rightarrow \Omega \text{ for } t \in R\}$ a family of measure-preserving mapping such that $(t, \omega) \rightarrow \theta_t \omega$ is measurable and satisfies

$$\theta_0 = I (\text{Identity mapping}), \quad (11)$$

$$\theta_{t+s} = \theta_t \circ \theta_s, \quad t, s \in R. \quad (12)$$

For the Wiener process $w(t, \omega) = \omega(t)$, the shift $\theta_t$ acts in such a way that

$$w(t, \theta_s \omega) = w(t + s, \omega) - w(s, \omega). \quad (13)$$

It should be noted that $w(t, \theta_s \omega)$ defined by (13) is also Wiener process.

Using the shift $\theta_t(\omega)$, the RDS on $R^n$ is defined.

**[Definition 1] The RDS (Random Dynamical System):** The RDS on $R^n$ over $(\Omega, \mathcal{F}, P, \{\theta_t\}_{t \in R})$ is the measurable mapping $\phi$:

$$\phi: \Omega \times R^n \rightarrow R^n, \quad (14)$$

$$\phi: (t, \omega, x) \rightarrow \phi(t, \omega, x) \equiv \varphi(t, \omega)x, \quad (15)$$

which satisfies

(a) $\phi$ is cocycle, i.e.,

$$\varphi(0, \omega)x = x, \quad (16)$$

$$\varphi(t + s, \omega)x = \varphi(t, \theta_s \omega)\varphi(s, \omega)x, \quad (17)$$

(b) $t \rightarrow \varphi(t, \omega)x$ is continuous, $x \rightarrow \varphi(t, \omega)x$ is smooth.

The RDS is the stochastic flow with the cocycle property. We explain the RDS for the $R^n$-valued stochastic system with $x(0, \omega) = x$ such that

$$dx(t, \omega) = f(x(t, \omega))dt + g(x(t, \omega))dw(t, \omega). \quad (19)$$

Denoting the solution of (19) by $\varphi(t, \omega)x$, $\varphi$ becomes the RDS generated by (19). And $\varphi(\tau - s, \theta_s \omega)x$ can be interpreted as the position at time $t = \tau$ of the trajectory which was at $x_s$ at time $t = s$. For the simplification of descriptions, we write $x(t)$ and $w(t)$ for $x(t, \omega)$ and $w(t, \omega)$ unless it causes confusion.

In the D-bifurcation analysis, the invariant measure plays a crucial role. In order to define the invariant measure, we introduce the skew product flow $\Theta_t(\omega, x)$ on $\Omega \times R^n$ defined by

$$\Theta_t(\omega, x) \equiv (\theta_t \omega, \varphi(t, \omega)x). \quad (20)$$

**[Definition 2] Invariant Measure:** For the RDS $\varphi$ on $\Omega \times \mathcal{F}, P, \{\theta_t\}_{t \in R}$, the probability measure $\mu$ on $\Omega \times R^n$ is called the invariant measure if $\mu$ satisfies

(i) $\Theta_t \mu = \mu$,

(ii) The marginal of $\mu$ on $\Omega$ is $P$.

The invariant measure $\mu$ can be uniquely factorized [6]:

$$\mu(d\omega, dx) = \mu_\omega(dx)P(d\omega). \quad (23)$$

where $\mu_\omega$ is a probability measure on $R^n$ for each fixed $\omega$. Since by the factorization (23), the invariance of the measure $\mu$ can be described as

$$\varphi(t, \omega)\mu_\omega = \mu_{\theta t \omega}, \quad P-a.s., \quad (24)$$

we call $\mu_{\omega}$ the invariant measure in what follows.

A probability measure $\rho$ on the measurable space $(R^n, B)$ is called stationary if the following holds

$$\rho(\cdot) = \int_{R^n} P(t, x, \cdot)\rho(dx), \forall t > 0, \quad (25)$$

where

$$P(t, x, B) = P\{\omega : \varphi(t, \omega)x \in B\}. \quad (26)$$

It should be noted that $\rho$ is the stationary solution of the Fokker-Planck equation.

Define $\mathcal{F}^\omega \equiv \sigma\{w(s) | s \leq 0\}$, then there is a one-to-one correspondence between the stationary measure $\rho$ and the $\mathcal{F}^\omega$ measurable invariant measure $\mu_{\omega}$ [6]:

$$\lim_{t \rightarrow \infty} \varphi(t, \theta_- \omega)\rho = \mu_{\omega}, \quad P-a.s., \quad (27)$$

$$E\{\mu_{\omega}\} = \rho. \quad (28)$$

The calculation defined by (27) is called pullback and an $\mathcal{F}^\omega$ measurable invariant measure $\mu_{\omega}$ can be calculated by pullback. In the bundle $\Omega \times R^n$, the mapping $\varphi(t, \theta_- \omega)$ is made to start at an earlier time as increasing time $t$, and the invariant measure $\mu_{\omega}$ is produced by making the stationary measure $\rho$ pulled back as shown in Fig. 2.

![Fig. 2 Generation of the invariant measure by pullback (cited from [8])](image)

**[Definition 3] D-bifurcation:** Let $\{\varphi_b\}_{b \in R}$ be a family of the RDS with invariant measures $\mu_b$. Then,
(b^*,μ_{b^*}) is called the D-bifurcation point if in each neighborhood of b^*, there is a b for which there exists an invariant measure \nu_b \neq \mu_b with \nu_b \rightarrow \mu_b as b \rightarrow b^*.

It follows from the Multiplicative Ergodic Theory (MET) \cite{6,10} that the Lyapunov exponent \lambda_i (i=1,2) of the stochastic system (19) under n=2 is given by

\lambda_i = \lim_{t \rightarrow \infty} \frac{1}{t} \log ||g(t)||, (i=1,2), \text{ P-a.s.}, \quad (29)

where \( g(t) \) is the solution of the following linearized equation of (19) with \( g(0) \neq 0 \) and \( g(0) \in V_i \) and where \( V_1 \oplus V_2 = R^2 \):

\[ dy^*(t) = Df(x(t))y^*(t)dt + Dg(x(t))y^*(t)dw(t). \quad (30) \]

It should be noted that the Lyapunov exponent \( \lambda_1(\lambda_2) \) in (29) is calculated using the solution of (30) with the nonzero initial condition \( y^*(0) \) belongs to the space \( V_1(V_2) \).

Since it is known that in the D-bifurcation point, one Lyapunov exponent necessarily vanishes \cite{6}, if there exists a bifurcation parameter which satisfies \( \lambda_1 = 0 \), its parameter value becomes the D-bifurcation point. On the other hand, if the Lyapunov exponent \( \lambda_1 \) does not change the sign, the D-bifurcation does not occur.

[Definition 4] Random Attractor: A random compact subset \( A(\omega) \) of \( R^n \) which satisfies below is called the random attractor:

(i) \( \varphi(t,\omega)A(\omega) = A(\theta_t\omega) \), \quad (31)

(ii) \( \lim_{t \rightarrow \infty} d(\varphi(t,\theta_{-t}\omega)B, A(\omega)) = 0 \), \( B \in B \), \quad (32)

where \( d(\cdot,\cdot) \) denotes the Hausdorff semimetric.

An important property of the random attractor is that all invariant measures necessarily have their supports in the random attractor.

4.2 The P-bifurcation

In this section, we explain the P-bifurcation. The P-bifurcation has the advantage of being visually understandable, however, the P-bifurcation is a static concept because it is defined by the the stationary probability density function (s-pdf) based on the one point motion.

[Definition 5] The P-bifurcation: Let \( \{\rho_b(x)\}_{b \in R} \) be a family of the s-pdf. Then, \( (b^*, \rho_{b^*}) \) is called the P-bifurcation point if the s-pdf changes qualitatively at \( b = b^* \), for instance, from unimodal to bimodal distributions.

For the stochastic system (19), the s-pdf \( \rho(x) \) is given by the solution of the stationary Fokker-Planck equation:

\[ -\sum_{i=1}^{n} \frac{\partial (\rho f_i)}{\partial x_i} + \frac{1}{2} \sum_{i,j=1}^{n} \frac{\partial^2 (\rho gg'_i)}{\partial x_i \partial x_j} = 0. \quad (33) \]

It should be noted that there is one-to-one correspondence (28) between an \( \mathcal{F}^- \) measurable invariant measure \( \mu_\omega \) and the s-pdf \( \rho \) given by the solution of (33).

The stationary Fokker-Planck equation for the stochastic plankton-fish system (4) and (5) is as follows:

\[ -\frac{\partial}{\partial x} \left\{ \rho(x,y) \left( ax(1-x) - \frac{xy}{h+x} \right) \right\} \]

\[ -\frac{\partial}{\partial y} \left\{ \rho(x,y) \left( \frac{bxy}{h+x} - my - f \frac{ny^2}{n^2+y^2} \right) \right\} \]

\[ + \frac{1}{2} \alpha^2 \frac{\partial^2}{\partial x^2} \left( \rho(x,y)x^2 \right) + \alpha \beta \frac{\partial^2}{\partial x \partial y} \left( \rho(x,y)xy \right) \]

\[ + \frac{1}{2} \beta^2 \frac{\partial^2}{\partial y^2} \left( \rho(x,y)y^2 \right) = 0. \quad (34) \]

If we introduce two independent environmental fluctuations for both plankton, the cross term (the 4th term of (34)) disappears. Since the cross term has little influence on the P-bifurcation analysis, the results obtained in this paper do not change in the two independent noise case.

Since the fish density \( f \) is a bifurcation parameter and the s-pdf \( \rho(x,y) \) is two-dimensional, if the shape of \( \rho(x,y) \) changes from unimodal to crater-like (or vice versa) with the change of \( f \), we conclude that the P-bifurcation occurs in the stochastic plankton-fish system (4) and (5).

5. Numerical Simulations

In this section, using the same values of parameters as in Fig. 1, i.e., \( a = 5.0, b = 1.0, h = 0.2, m = 0.6, n = 0.4 \), we analyze numerically the influence of the random noise on the Hopf bifurcation by the D- and the P- bifurcations. Denoting the deterministic Hopf bifurcation point given by the filled rectangle in Fig. 1 as \( f^* \), we have \( f^* = 0.328 \). Under the noise coefficient \( \alpha = \beta = 0.005 \) in (4) and (5), we perform numerical simulations using the Euler method with the order 0.5 and the time step \( \Delta t = 0.001 \).

5.1 The D-bifurcation Analysis

Since it is known that the result of the pullback does not depend on the initial values, we consider the uniform distribution as the initial value and its support is given by the uppermost, left-hand side column in Fig. 3.

(i) \( f = 0.20 < f^* \): In this case, the deterministic coexistent steady state becomes unstable spiral. As shown in Fig. 3, a circle appears in a comparatively short time and converges to the random point \( \xi(\omega) \) on the circle after long time. So, we have

\[ \lim_{t \rightarrow \infty} \varphi(t,\theta_{-t}\omega)(x,y) = \xi(\omega), \text{ P-a.s.}, \quad (35) \]

It follows from convergence of the support of \( \mu_\omega \) to one random point \( \xi(\omega) \) that the invariant measure \( \mu_\omega \) is given by

\[ \mu_\omega = \delta(x-\xi(\omega)). \quad (36) \]

(ii) \( f = 0.45 > f^* \): In this case, the determinis-
The coexistent steady state becomes stable spiral. We show the behavior of \( \varphi(t, \theta_{-}\omega)(x, y) \) in Fig. 4. As shown in Fig. 4, since \( \varphi(t, \theta_{-}\omega)(x, y) \) converges to the random point \( \zeta(\omega) \), the invariant measure \( \mu_{\omega} \) becomes

\[
\mu_{\omega} = \delta(x - \zeta(\omega)).
\]

(37)

Since the D-bifurcation point accords with the parameter value at which the Lyapunov exponent of the invariant measure disappears. Using (29) and (30), the Lyapunov exponents \( \lambda_i \) is given by

\[
\lambda_i = \lim_{t \to \infty} \frac{1}{t} \ln \| z(t) \|, z(0) \neq 0 \in V_i, \ (i = 1, 2). \tag{38}
\]

where \( V_1 \oplus V_2 = R^2 \) and \( z(t) = [x(t) \quad y(t)]' \) is the solutions of the linearized equations:

\[
dx(t) = \left\{ a(1 - 2u(t)) - \frac{hv(t)}{u(t) + h^2} \right\} x(t)dt
\]

(39)

\[
dy(t) = \frac{bhv(t)}{(u(t) + h)^2} x(t)dt + \left( \frac{bu(t)}{u(t) + h} - m \right) y(t)dt
\]

(40)

Using (38) to (42), we show the \( f \)-dependency of the Lyapunov exponents in Fig. 5. In numerical calculations, using the Gram-Schmidt orthonormalization [16], we calculate the Lyapunov exponents under the initial values \( V_1 = [1 \ 0]' \), \( V_2 = [0 \ 1]' \) in (38). In Fig. 5, the red line is the biggest Lyapunov exponent and the blue one is the second one. The lower figure of Fig. 5 is the magnified figure of Lyapunov exponents in the neighborhood of zero. In the deterministic system (6) and (7), the stability of the coexistent

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Fig. 3 Time evolution of \( \varphi(t, \theta_{-}\omega)(x, y) \) (\( f = 0.20 \))

Fig. 4 Time evolution of \( \varphi(t, \theta_{-}\omega)(x, y) \) (\( f = 0.45 \))
state \((u_e,v_e)\) changes from unstable spiral to stable spiral at the Hopf bifurcation point \(f = f^*\). On the other hand, in the stochastic system (4) and (5), both Lyapunov exponents are always negative. This fact implies that the D-bifurcation does not occur in the stochastic plankton-fish system considered here.

5.2 The P-bifurcation Analysis

We can study the P-bifurcation by solving the stationary FPK equation (34), however, since (34) is not elliptic because the rank of the diffusion matrix \((gg')\) in (33)) is 0 or 1, it is not easy to solve (34), especially in the case where \(\alpha\) and \(\beta\) are comparatively small. Hence, we consider the scatter diagram of the 2000-sample paths with the same initial condition, and calculate the frequency distribution [17]. By normalizing the frequency distribution, we have the approximate s-pdf (stationary probability density function).

Setting the initial values as \(u(0) = 0.5\), \(v(0) = 0.3\) and the values of the noise coefficient \(\alpha = \beta = 0.005\), we calculate the scatter diagram of the 2000-sample paths with the fish densities \(f = 0.30, 0.33, 0.35, 0.40, 0.45, 0.48\) at time \(t = 2000\), the results are shown in Fig. 6. From Fig. 6, we can see that the scatter diagram changes from circle-like to the small point as the fish density \(f\) increases. Based on Fig. 6, we compute the frequency distribution. The results after normalization are shown in Fig. 7. Figure 7 shows the approximate s-pdf. From Fig. 7, we can see that the approximate s-pdf changes from crater-like to unimodal with the change of the fish density \(f\), hence, we conclude that the P-bifurcation occurs in the stochastic plankton-fish system considered here.

6. Conclusions

In the bifurcation analysis of the stochastic system, there exist two approaches. One is the D-bifurca-
tion approach that studies the stability of the invariant measure. The other is the P-bifurcation approach that studies the qualitative change in the shape of the stationary measure, which is given as the solution of the stationary Fokker-Planck equation. The difference between the D- and the P-bifurcation approaches is that the former approach is based on the concept of the random dynamical system describes the behavior of many points, the latter studies the behaviors of many sample paths of one point.

By the numerical simulations, we have shown that the Lyapunov exponents are always negative in the stochastic plankton-fish system considered here, so that the D-bifurcation does not occur in the stochastic case. It should be noted that the Hopf bifurcation occurs in the corresponding deterministic system. Hence, even if the strength of the random noise is comparatively small, it has a great effect on the plankton-fish system from the point of view of the P-bifurcation. In the stochastic plankton-fish system, the process $\phi(t,\theta, \omega)(x,y)$ eventually converges to a random point as $t \rightarrow \infty$ independently of the value of the fish density $f$. This fact means that the random attractor in the stochastic plankton-fish system considered here is a point set consisting of a random point.

On the other hand, in the P-bifurcation approach, since it is difficult to solve the stationary Fokker-Planck equation because it is not elliptic and the coefficients of diffusion terms are comparatively small, we can calculate the scatter diagram of sample paths with the same initial condition, and derive the frequency distribution. By normalizing the frequency distribution, we have obtained the approximate s-pdf. And we have shown that the shape of the approximate s-pdf changes from the crate-like to the peak-like one with the change of the fish density $f$. This fact implies that the P-bifurcation occurs in the stochastic plankton-fish system as well as the deterministic one. Moreover, we confirm that the P-bifurcation occurs under the stronger strength of the random noise. Hence, the effect of the random noise on the fish-plankton system is little from the viewpoint of the P-bifurcation.

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