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SIMULATION ANALYSIS OF SPATIO-TEMPORAL PATTERNS IN STOCHASTIC PLANKTON-FISH SYSTEMS

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Abstract. *An ecosystem consists of a large variety of species and creatures interact with each other by means of a food chain. Since behaviors of some species in the food chain have an effect on the whole ecosystem, it is very important to consider spatio-temporal change of the populations of species from the view point of ecosystem management and protection. In this paper, we consider the food chain consisting of three populations, fish, zooplankton and phytoplankton, and study the modeling of such a food chain and analyze their spatio-temporal behaviors by numerical simulations. Environmental changes in the food web 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. Thus, we propose the stochastic plankton-fish model. In the numerical analyses of the stochastic plankton-fish system, we show that the size, motion and geometrical shape of fish school have a great influence on emergence of a spiral wave in the plankton-fish system and such a spiral is robust for disturbance.*
Keywords: Stochastic predator-prey system, Plankton-fish system, Spatio-temporal patterns, Spiral wave, Bifurcation, Numerical simulations

1. **Introduction.** A wide variety of spatio-temporal behaviors of organisms are observed in nature and the analysis of such behaviors has been one of important problems in bioecology [1-6]. So far, a large number of analytical models in ecology have been proposed in the past. With help from differential equations, fuzzy theory, cellular automata and others, the behavior of spatially homogeneous population in ecosystem has been studied. However, most of conventional models are deterministic, and even if the models are stochastic, they are non-diffusive. Since in ecosystem, some sort of random fluctuation is often caused by environmental change, a practical analysis of ecosystem requires a stochastic model. In the real world, the populations of ecological species vary not just temporally but spatially because of environmental change such as weather and the spatial migration of species. Hence, we need to take into account spatial movement of each population for a practical study of ecosystem. For these reasons, we consider a stochastic diffusive modeling of ecosystem. Especially, we study a stochastic diffusive plankton-fish system for the following reasons. Since red tide has caused large-scale fishkill and gives severe damage to commercial fisheries, it is extremely important to take effective countermeasures against the red tide problem. Red tide is caused by a population explosion of toxic plankton. The spatio-temporal patterns in the plankton-fish system are closely related to outbreak of red tide. Furthermore, since the presence of noise can change the stability and behaviors of the corresponding deterministic systems [3,4,7], the influence analysis of noise on the plankton-fish system is crucial for the practical study of ecosystem. Hence,

we study the spatio-temporal behaviors of plankton in the stochastic plankton-fish system with diffusion by the numerical simulations.

We begin with the explanation of the conventional deterministic plankton-fish model with diffusion [8-11] in Section 2. In Section 3, we propose the stochastic diffusive plankton-fish model. Since the behavior of plankton in the stochastic diffusive plankton-fish model has a strong relation to the stability of the steady state of the corresponding deterministic non-diffusive model, we study the stability of the spatially uniform steady state in Section 4. In Section 5, we analyze the influence of the random noise and the size of fish school on the spatio-temporal behavior of plankton by simulations. Finally, we summarize the results obtained in this research in Section 6.

2. Deterministic Plankton-fish System.

The conventional plankton-fish model [8-11] is given below:

$$\frac{\partial u(t,x)}{\partial t} = d_u \Delta u(t,x) + s(u(t,x)) - \ell(u(t,x))v(t,x), \tag{1}$$

$$\frac{\partial v(t,x)}{\partial t} = d_v \Delta v(t,x) + \ell(u(t,x))v(t,x) - mv(t,x) - e(v(t,x))f(t,x), \tag{2}$$

where $u(t,x)$ and $v(t,x)$ are the densities of phytoplankton and zooplankton at time $t \in \Theta \equiv (0,T)$ and position $x \in G$, d_u and d_v are their diffusion coefficients, $s(u)$, $\ell(u)$ and $e(v)$ denote the proliferation of phytoplankton, the predation rate of phytoplankton by zooplankton and the predation rate of zooplankton by fish, $f(t,x)$ and m are the fish density and the natural death rate of zooplankton, respectively.

Generally, it is plausible that fish is considered as localized in a school and is rather difficult to incorporate the fish behavior by an equation-based approach. Therefore, we consider the fish as a discrete rule-based agent. The concrete rules are specified in Section 5.

As the proliferation of phytoplankton, we apply the logistic function:

$$s(u) = ru(1-u), \tag{3}$$

where r is a positive constant.

In Equations (1) and (2), functions $\ell(u)$ and $e(v)$ are called the functional responses of predators and their typical forms are shown in Figure 1. The functional response $F(x)$ of Holling type I means that the predation rate is proportional to the prey density. In the Holling types II and III, each predation rate increases to their saturation values. The curves of types II and III differ in that the former is concave, while the latter has an inflection point.

$$\text{Holling type I: } F(x) = ax, \tag{4}$$

$$\text{Holling type II: } F(x) = \frac{ax}{a+bx}, \tag{5}$$

$$\text{Holling type III: } F(x) = \frac{b^2x^2}{1+a^2x^2}. \tag{6}$$

According to [8-11], we apply Holling types II and III as the predation rate of zooplankton and fish, respectively:

$$\ell(u) = \frac{au}{1+bu}, \quad e(v) = \frac{g^2v^2}{1+h^2v^2}, \tag{7}$$

where a, b, g and h are positive constants.

Using Equations (3) and (7) to Equations (1) and (2), we have

$$\frac{\partial u(t,x)}{\partial t} = d_u \Delta u(t,x) + ru(t,x)(1-u(t,x)) - \frac{au(t,x)}{1+bu(t,x)}v(t,x), \tag{8}$$

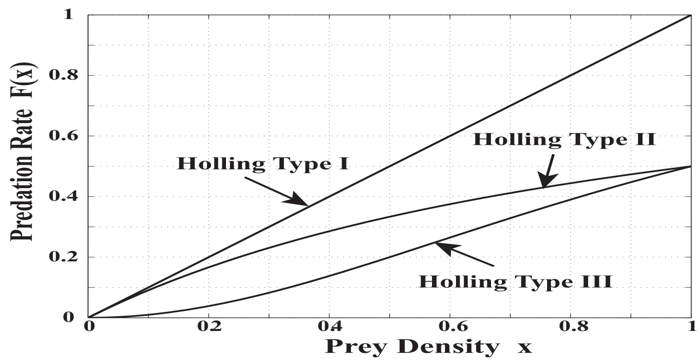


FIGURE 1. Functional responses of Holling type

$$\frac{\partial v(t,x)}{\partial t} = d_v \Delta v(t,x) + \frac{au(t,x)}{1+bu(t,x)} v(t,x) - mv(t,x) - \frac{g^2 v(t,x)^2}{1+h^2 v(t,x)^2} f(t,x). \tag{9}$$

We impose the following initial and boundary conditions on $u(t,x)$ and $v(t,x)$:

$$u(0,x) = u_0(x), \quad v(0,x) = v_0(x), \quad x \in G, \tag{10}$$

(Zero Flux B.C.)

$$\frac{\partial u(t,x)}{\partial \nu} = \frac{\partial v(t,x)}{\partial \nu} = 0, \quad (t,x) \in \Theta \times (\Gamma_1 \cup \Gamma_2), \tag{11}$$

(Periodic B.C.)

$$u(t,x) = u(t,y), \quad \frac{\partial u(t,x)}{\partial \nu} = \frac{\partial u(t,y)}{\partial \nu}, \quad (t,x) \in \Theta \times \Gamma_3, \quad (t,y) \in \Theta \times \Gamma_4, \tag{12}$$

$$v(t,x) = v(t,y), \quad \frac{\partial v(t,x)}{\partial \nu} = \frac{\partial v(t,y)}{\partial \nu}, \quad (t,x) \in \Theta \times \Gamma_3, \quad (t,y) \in \Theta \times \Gamma_4, \tag{13}$$

where $\{\Gamma_i\}_{i=1}^4$ denote the boundary ∂G of G such that $\partial G = \cup_{i=1}^4 \Gamma_i, \Gamma_i \cap \Gamma_j = \emptyset \ (i \neq j)$ and $\partial(\cdot)/\partial\nu$ is an exterior normal derivative at ∂G.

We assume that fish school follows the same boundary conditions as Equations (11)-(13).

3. **Stochastic Plankton-fish Model.** In this section, we propose the stochastic diffusive plankton-fish model so as to study the influence of the random noise on the behavior of each plankton. We model such a noise by the spatio-temporal Gaussian white noise [12] and consider the stochastic model with the same initial and boundary conditions as the deterministic model:

$$\frac{\partial u(t,x)}{\partial t} = d_u \Delta u(t,x) + ru(t,x)(1-u(t,x)) - \frac{au(t,x)}{1+bu(t,x)} v(t,x) + \alpha u(t,x)\eta(t,x), \tag{14}$$

$$\frac{\partial v(t,x)}{\partial t} = d_v \Delta v(t,x) + \frac{au(t,x)}{1+bu(t,x)} v(t,x) - mv(t,x) - \frac{g^2 v(t,x)^2}{1+h^2 v(t,x)^2} f(t,x) + \beta v(t,x)\xi(t,x), \tag{15}$$

where $\eta(t,x)$ and $\xi(t,x)$ are mutually independent spatio-temporal Gaussian white noises with zero mean and covariance:

$$E\{\eta(t,x)\eta(\tau,y)\} = \delta(t-\tau)\delta(x-y), \tag{16}$$

$$E\{\xi(t,x)\xi(\tau,y)\} = \delta(t-\tau)\delta(x-y). \tag{17}$$

4. **Stability Analysis.** The behavior of the solution of the stochastic model (14) and (15) is closely related to the stability of the spatially uniform steady state of the following deterministic system with the constant fish density $f(t,x) = f$:

$$\frac{du(t)}{dt} = ru(t)(1-u(t)) - \frac{au(t)}{1+bu(t)}v(t), \tag{18}$$

$$\frac{dv(t)}{dt} = \frac{au(t)}{1+bu(t)}v(t) - mv(t) - \frac{g^2v(t)^2}{1+h^2v(t)^2}f. \tag{19}$$

It is easily shown that Equations (18) and (19) have three steady states $(\bar{u},\bar{v})$ such that

$$(\bar{u},\bar{v}) = (0,0),\ \ (1,0),\ \ (u_*,v_*), \tag{20}$$

where (u_*,v_*) denotes the coexistent steady state defined by

$$u_* = \frac{m + f\frac{g^2v_*}{1+h^2v_*^2}}{a - b\left(m + \frac{fg^2v_*}{1+h^2v_*^2}\right)},\quad v_* = \frac{r}{a}(1-u_*)(1+bu_*). \tag{21}$$

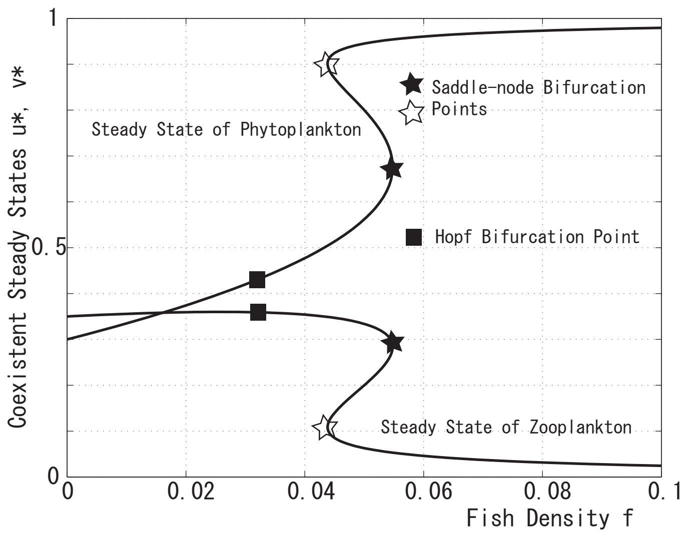


FIGURE 2. Dependency of the coexistent steady state (u_*,v_*) on the fish density f

The dependency of the coexistent steady state (u_*,v_*) on the fish density f is shown in Figure 2. In Figure 2, parameter values are set as $r = 1.0$, $a = b = 5.0$, $m = 0.6$, $g = h = 10.0$. As shown in Figure 2, at the high fish density, phytoplankton-dominated state is the steady state. As lowering f, two steady states appear by the saddle-node bifurcation [13] at the point of the filled star in Figure 2, 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 square in Figure 2, the Hopf bifurcation [13,14] 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.

5. **Simulations.** Setting the parameter values as $d_u = d_v = 0.005$, $\alpha = \beta = 0.008$, $r = 1.0$, $a = b = 5.0$, $m = 0.6$, $g = h = 10.0$, numerical simulations are performed under the initial conditions $u_0(x_1, x_2) = 0.4$, $v_0(x_1, x_2) = 0.6$ in the square region $G \equiv (x_1, x_2) \in (0, 40) \times (0, 40)$. In Equations (11)-(13), the boundary $\partial G = \cup_{i=1}^4 \Gamma_i$ is defined in such a way that $\Gamma_1 = (0, x_2)$ and $\Gamma_2 = (40, x_2)$ for $x_2 \in (0, 40)$, $\Gamma_3 = (x_1, 0)$ and $\Gamma_4 = (x_1, 40)$ for $x_1 \in (0, 40)$.

We assume that fish schools move on the numerical grids according to the following rules [10]:

(i) The fish schools feed on zooplankton down to its protective minimal density v_m and then move.
(ii) The fish schools have maximal residence time due to the protection against higher predator.
(iii) The fish schools memorizes and prefer the previous direction of motion. The following direction is randomly chosen as shown in Figure 3.

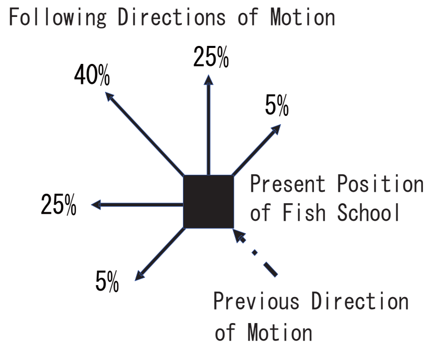
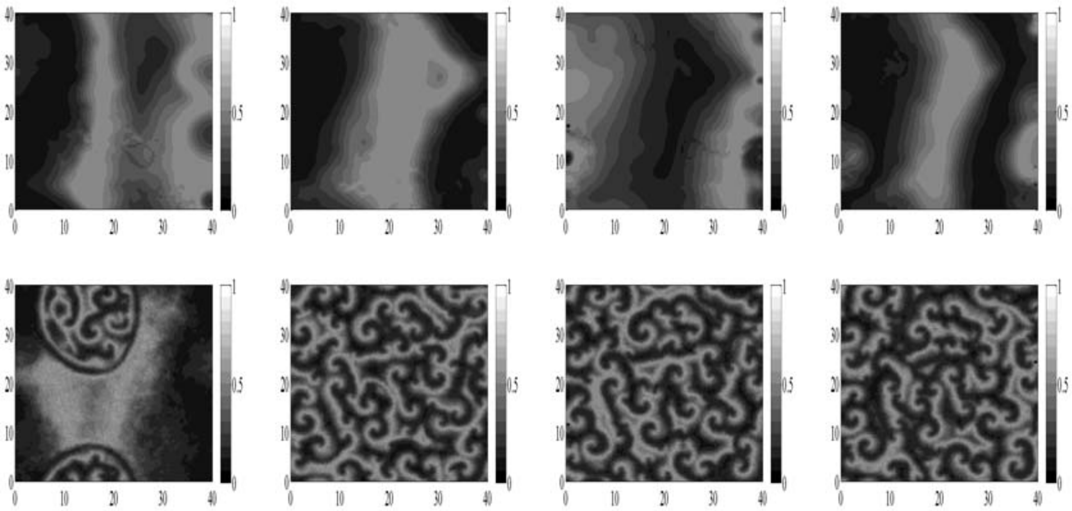


FIGURE 3. Movement probability to the following direction

In the numerical simulations, the size of fish school means the number of numerical grids contained in fish school. Changing the size of fish school, we study the influence of the random noise and the movement of fish school on the spatio-temporal behaviors of plankton.

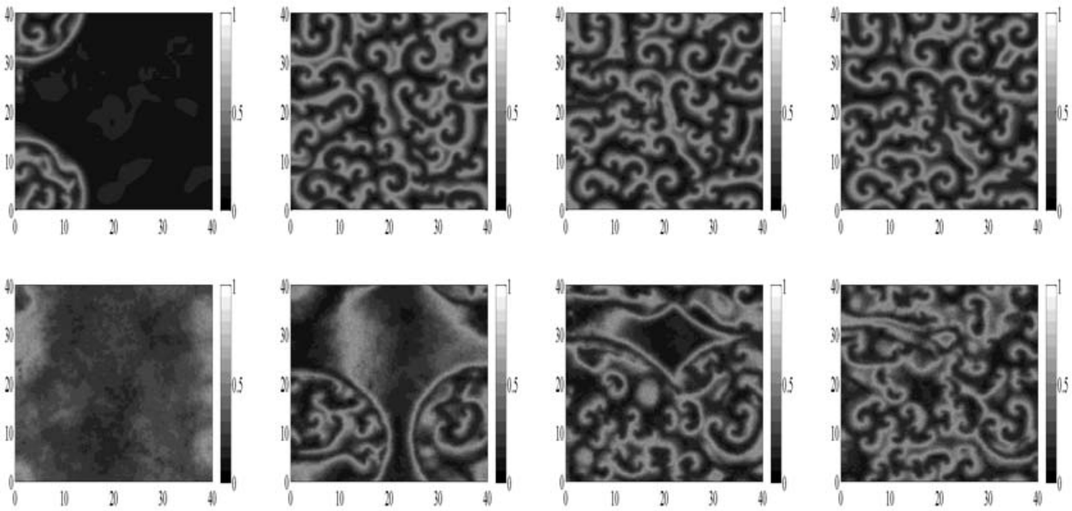
(Case 1) *Three Fish Schools with the size of* 2×2 *grids*:
Simulation results in this case are shown in Figure 4. Since the behavior of phytoplankton shows a similar feature to the zooplankton behavior, the results of phytoplankton are omitted here. In Figure 4, the zooplankton density is shown by a gray scale: the white part denotes the region with the high zooplankton density. The upper and the lower figures at each time are results under no noise and noise, respectively. It follows from Figure 4 that the behavior of zooplankton under no noise seems temporally periodic (i.e., black and white regions counterchange with time) and no spatial pattern appears, whereas under noise, the region with the high zooplankton density forms the spiral structure. Thus, we presume that the spiral structure in this case is induced by the random noise. Once the spiral wave is formed, the spiral is robust for the random noise as shown in Figure 4.

(Case 2) *Three Fish Schools with the size of* 3×3 *grids*:
Number of fish school in Case 2 is the same as Case 1, however, the size of fish school is larger than Case 1. As shown in Figure 5, the spiral structure is formed under both the no noise and the noise cases. The spiral wave under no noise appears earlier than under noise. Thus, we presume that the spiral structure in this case is induced by the movement of fish school unlike in Case 1 and the appearance of the spiral induced by the fish motion is disturbed by the random noise. However, once the spiral is formed, it is robust for the random noise as well as Case 1.



$t = 10840$ $t = 14020$ $t = 14380$ $t = 14740$

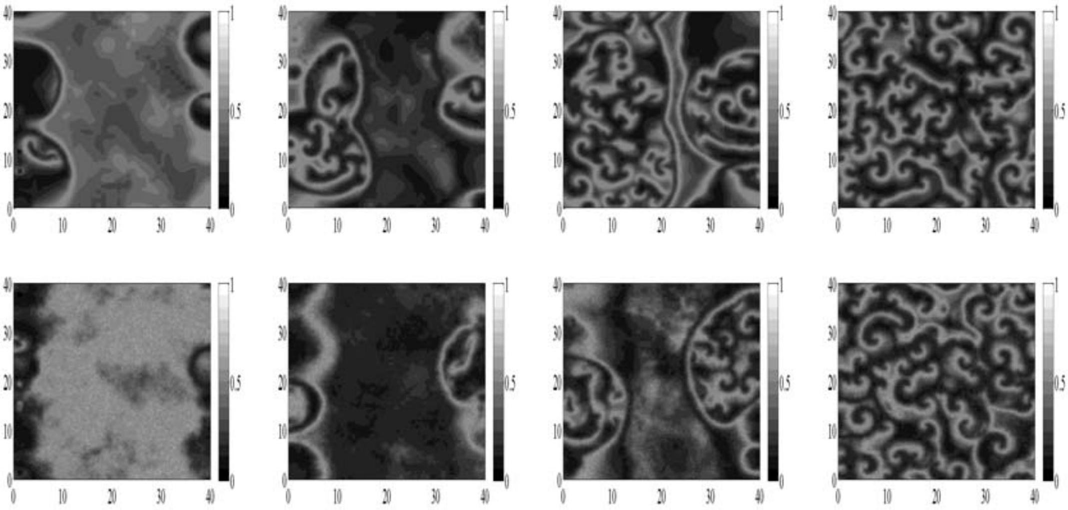
FIGURE 4. Spatio-temporal patterns of zooplankton density $v(t, x)$ under 3 schools with the size of 2×2 grids



$t = 1200$ $t = 4260$ $t = 4620$ $t = 4840$

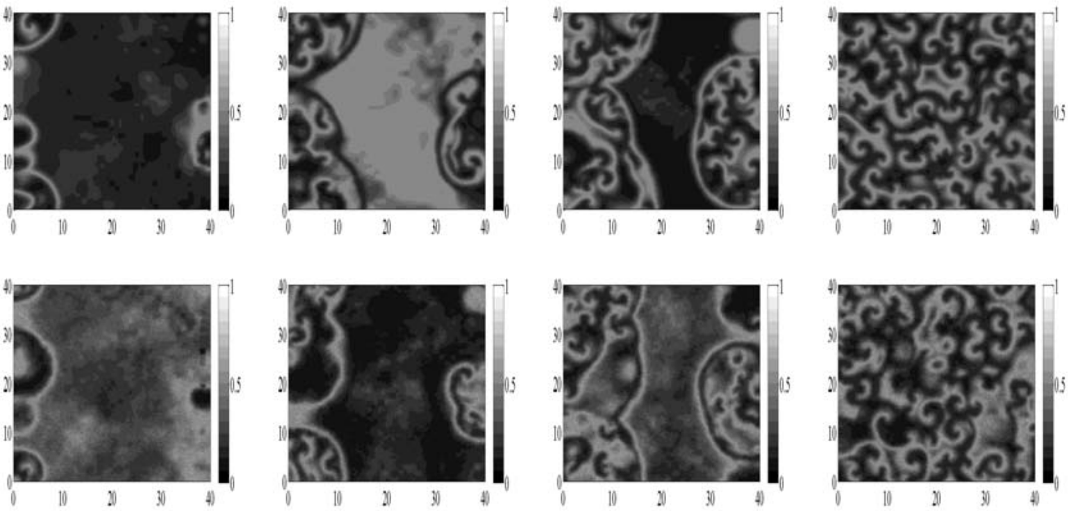
FIGURE 5. Spatio-temporal patterns of zooplankton density $v(t, x)$ under 3 schools with the size of 3×3 grids

(Case 3) *Three Fish Schools with the size of* 4×4 *grids*:
In Case 3, we consider fish school with the same number of school as Cases 1 and 2, however, the size of fish school is larger than Cases 1 and 2. Simulation results in this case are shown in Figure 6. Figure 6 shows that the spiral structure appears in both the no noise and the noise cases as well as Case 2, however, onset of the spiral structure is much earlier than Case 2 independently of the presence or absence of noise.
(Case 4) *Three Fish Schools with the size of* 5×5 *grids*:
In Case 4, although the number of fish school is the same as the previous cases, the size of fish school is larger than other cases. Simulation results in Case 4 are shown in Figure 7.



$t = 760$ $t = 1100$ $t = 1480$ $t = 2860$

FIGURE 6. Spatio-temporal patterns of zooplankton density $v(t, x)$ under 3 schools with the size of 4×4 grids



$t = 580$ $t = 940$ $t = 1200$ $t = 2160$

FIGURE 7. Spatio-temporal patterns of zooplankton density $v(t, x)$ under 3 schools with the size of 5×5 grids

In this case, the spiral structure appears under both no noise and noise as well as Cases 2 and 3. However, onset of the spiral structure is much earlier than Cases 2 and 3. Results of Cases 1 to 4 show that the spiral wave is likely to develop as the size of fish school increases and the spiral structure is robust for the random noise.

(Case 5) *Three Fish Schools with the size of* 1×4 *grids*:

As shown in Figure 4, three fish schools with the size of 2×2 grids in Case 1 are not able to induce the spiral structure under no noise. In Case 5, we study the influence of a geometric anisotropy of fish school on the behavior of each plankton. We consider three fish schools with the same size as Case 1, but anisotropic shapes. Simulation results

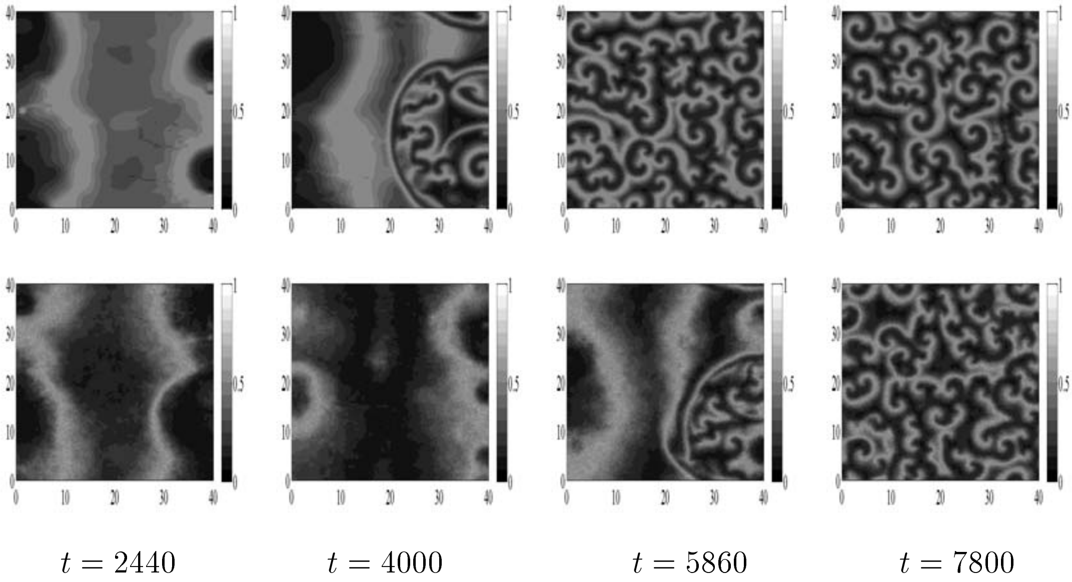


FIGURE 8. Spatio-temporal patterns of zooplankton density $v(t, x)$ under 3 schools with the size of 1×4 grids

are shown in Figure 8. Although the number of fish school and its area are the same as Case 1, the spiral structure appears in both the no noise and the noise cases. Thus, the geometric anisotropy of fish school seems to induce the emergence of the spiral structure.

6. Conclusions.

In this paper, taking the random fluctuation caused by the environmental change into consideration, we have proposed the stochastic diffusive plankton-fish model. Using the proposed stochastic model, we have studied the influences of the movement of fish school and the spatio-temporal noise on behaviors of plankton by numerical simulations. Results in our numerical simulations have shown that the random noise and the fish school motion are able to induce the spiral structure in the plankton distribution if the size of fish school is appropriate. Even if the fish school motion is not able to induce such a spiral structure, the spatio-temporal noise is able to produce the spiral in some cases.

We have clarified that once the spiral is formed, it is robust for the spatio-temporal noise. Besides simulations results have shown that as the size of fish school increases, the initiation of the spiral structure is becoming earlier.

Moreover, the anisotropy of fish school seems to have a strong relation to the emergence of such a spiral pattern. The anisotropy of fish school promotes an appearance of the spiral structure.

In the plankton-fish system considered in this paper, if fish school stays at some spatial position, the target pattern (concentric circle pattern) of the plankton density is produced. In numerical simulations, since fish do not stay at one position for a long time, although we cannot observe the complete target pattern, it follows from observations in numerical simulations that the breakup of the target pattern seems to induce the spiral structure. Such a breakup arises from the presence of noise and/or the fish school motion.

The unique features and the main advantages of this research are described below: To the best of our knowledge, this paper is the first work that has revealed the interaction between behaviors of plankton, geometric properties of fish school and the random noise in environment. Since the conventional works for the plankton-fish system have been done in deterministic diffusive, deterministic non-diffusive, or stochastic non-diffusive models, the conventional models are inadequate to study practical plankton-fish systems because fish and plankton move spatially and environmental changes cause the random fluctuation in the practical system. Hence, our research by the stochastic diffusive plankton-fish model is more practical than the conventional studies. Furthermore, since the presence of noise can change the stability and behaviors of the corresponding deterministic systems [4,6,7], the influence analysis of noise on the plankton-fish system is crucial for the practical study of ecosystem. Main contributions of this research to ecology and related research fields are that we have analyzed the spatio-temporal behavior of zooplankton and phytoplankton under the environmental fluctuation and have clarified how the spiral pattern is spatially and temporally formed. The analysis of the emergence of the spiral pattern contributes greatly to the study of the pattern formation problem in nature and plays an important role to take effective countermeasure against red tide problem.

The study of the stochastic bifurcation [15] and the bifurcation control [16] of the plankton-fish system are further research issues.

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