

Far-field breakup of spiral waves in the plankton ecological systems

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For oscillatory conditions, breakup of the spiral waves far away from the spiral core (as so-called “far-field breakup”) was reported in a simple activator-inhibitor model by Markus Bär, Michal Or-Guil and Lutz Brusch [Phys. Rev. Lett. **82**, 1160 (1999) and New J. Phys. **6**, 5 (2004)], which is in the chemical reaction-diffusion system. In present letter, the scenario in the plankton ecological system is reported. The spatial plankton model is studied numerically by computer and we find that the far-field breakup also exists in the oceanic ecological systems over a range of diffusion coefficients of phytoplankton and zooplankton. The far-field breakup leading to the spatial chaos patterns can be verified in field observation and is useful to understand the population dynamics of oceanic ecological systems. It also indicates that the far-field breakup may be a common phenomenon in the world. Finally, we give some illumination from the ecological meaning.

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There is growing interest in the spatial pattern dynamics of ecological systems [1–13]. The spatial distribution of natural population is usually remarkably inhomogeneous. In terrestrial ecosystems, the inhomogeneity of the spatial distribution of the population is to larger extent controlled by the inhomogeneity of the environment. Very high mobility of the marine environment would prevent the formation of any stable patch spatial distribution with much longer life-time than the typical time of biodynamics. However, in addition to very changeable transient spatial patterns, in marine environment there also exists other spatial patterns, much more stable spatial structure associated with ocean fronts, spatiotemporal chaos [10, 11], cyclonic rings, and so called meddies [14]. In fact, it is significant to create the biological basis for understanding spatial patterns of plankton [15]. During a long period of time, all the spiral waves have been widely observed in diverse physical, chemical, and biological systems [16–19]. However, a quite limited number of documents [11, 12, 20] concern the spiral waves and its breakup in the ecological systems.

The investigation of transition from regular patterns to spatiotemporally chaotic dynamics in extended systems remains a challenge in nonlinear science [16, 21, 22]. So far, there exists various, often heuristic explanations of the breakup phenomenon, most of which consider that the spiral core is a localized source of periodic waves. Far away from the core, the profile of the spirals approaches a planar periodic wave train with a wave number specific to the parameters of the system (wavelength selection). In general, breakup is attributed to the selection of a wave number that is too small to be sustained in the system. In Refs. [21, 22], it has been argued that the spiral wavelength is already too close to the minimum wavelength λ_{min} allowed by the dispersion relation for

wave trains in 1D, and two different breakup scenarios in the FitzHugh-Nagumo model. The oscillatory case shows the familiar breakup far away from the core and is related to the convective nature of the Eckhaus instability preceding the global mode instability necessary for breakup. Two main reasons for the spiral instability are found in Refs. [21, 22]: the absolute Eckhaus instability where the perturbations travel away from the spiral core and a novel finite-wavelength instability where perturbations travel towards the core. The latter instability causes spiral breakup near the core, whereas the absolute Eckhaus instability produces far-field breakup for sufficiently large group velocities of the outward propagating fastest growing modes. In this Letter, we find that far-field breakup of the spiral waves leading to turbulence also exhibits in the plankton model in the two dimensions under the sinusoidal oscillation rather than the relaxational oscillation with large amplitude.

We consider the 2D two-component basic marine food chain model, where at any point (X, Y) and the time τ , the dynamics of phytoplankton $P(X, Y, \tau)$ and zooplankton $H(X, Y, \tau)$ populations are given by the following reaction-diffusion equations [10, 11, 23, 24]:

$$\frac{\partial P}{\partial \tau} = RP(1 - \frac{P}{K}) - \frac{AC_1 P}{C_2 + P}H + D_P \nabla^2 P, \quad (1a)$$

$$\frac{\partial H}{\partial \tau} = \frac{C_1 P}{C_2 + P}H - MH - F \frac{H^2}{C_3 + H^2} + D_H \nabla^2 H. \quad (1b)$$

The parameters R , K , M , and $1/A$ denote the intrinsic growth rate and carrying capacity of phytoplankton and the death rate and yield coefficient of phytoplankton to zooplankton, respectively. The constants C_1 , C_2 , and C_3 parameterize the saturating functional response. F is the fish predation rate on zooplankton, and D_P and D_H are the diffusion coefficients of phytoplankton and zooplankton, respectively. $\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ is the two-dimensional Laplace operator. In model (1), the dependence of the zooplankton grazing rate on phytoplankton

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is of type II, while the zooplankton predation by fish follows a sigmoidal functional response of type III (see the Refs. [25, 26]). Following the Refs. [10, 11, 24], introducing $p = P/K$ and $h = AH/K$, time is scaled by a characteristic value of the phytoplankton growth rate R_0 . Space is scaled by the size of the numerical mesh L/j , where L is the total length of the considered area and $j + 1$ is the number of modes of the mesh. Thus, $x = jX/L$, and $t = R_0\tau$. The model (1) can be simplified by introducing dimensionless variables. As a result, Eqs. (1a) and (1b) become

$$\frac{\partial p}{\partial t} = rp(1-p) - \frac{ap}{1+bp}h + d_p\nabla^2 p, \quad (2a)$$

$$\frac{\partial h}{\partial t} = \frac{ap}{1+bp}h - mh - f\frac{nh^2}{n^2+h^2} + d_h\nabla^2 h, \quad (2b)$$

where the new parameters are $r = R/R_0$, $a = C_1K/(C_2R_0)$, $b = K/C_2$, $m = M/R_0$, $n = C_3A/K$, $d_p = j^2D_P/(LR_0)$, $d_h = j^2D_H/(LR_0)$, $f = FA/(C_3R_0)$ (similar to what is discussed in Ref. [10]).

The local dynamics are given by

$$g_1(p, h) = rp(1-p) - \frac{ap}{1+bp}h, \quad (3a)$$

$$g_2(p, h) = \frac{ap}{1+bp}h - mh - f\frac{nh^2}{n^2+h^2}. \quad (3b)$$

For the non-spatial system, from the earlier results [23] by using a numerical bifurcation analysis, we know that the bifurcation and bistability can be found in the system (3) when the parameters are within a realistic range. For the fixed parameters (see the caption of the Fig. 1), we can see that the f controls the distance from Hopf bifurcation (the Hopt onset is at $f_H = 0.445$ or $f_{H'} = 0.660$). The bistability will emerge when the parameter f is in the interval $f_{H'} > f > f_H$. There are three steady states: with these kinetics A and C are linearly stable while B is unstable. Outside this interval the system (1) has unique nontrivial fixed point.

Using our recent results (unpublished), the systems (2) can well-develop the spiral waves in the oscillation regime. Here we report the discovery of spatiotemporal chaos due to breakup in the system.

The simulation is done in a tow-dimensional (2D) Cartesian coordinate system with a grid size of 600×600 . The fourth order Runger-Kutta integrating method is applied with a time step $\Delta t = 0.005$ time unit and a space step $\Delta x = \Delta y = 0.20$ length unit. The results remain the same when checked by the simple Euler method. The diffusion terms in Eqs. (2a) and (2b) often describe the spatial mixing of species due to self-motion of the organism. Through the relationship between turbulent diffusion and the scale of the phenomenon in the sea [27], one can see that with the characteristic growth rate $R_0 = 10^{-5}s^{-1}$ [28] or one division per day, typical of

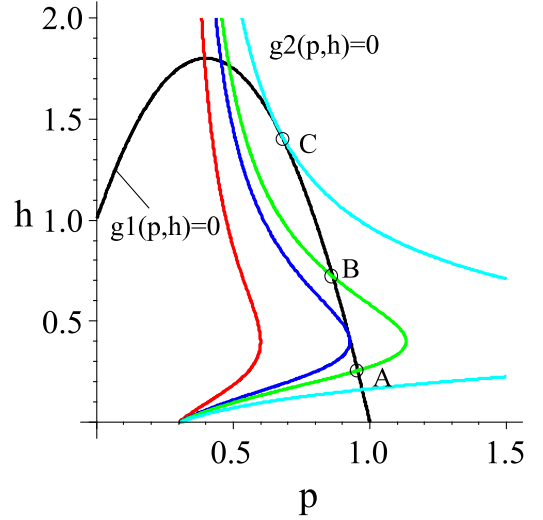


FIG. 1: The sketch map for the bistability and the Hopf bifurcation in the system (3) with $r = 5.0$, $a = 5.0$, $b = 5.0$, $m = 0.6$, and $n = 0.4$.

plankton patterns d_p is about 0.05. From the biological meaning, the diffusion coefficients should satisfy $d_h \geq d_p$. However, in nature waters it is turbulent diffusion that is supposed to dominate plankton mixing [29], the $d_h < d_p$ is allowed. We choose the d_h as the control parameter, keeping $d_p = 0.05$ throughout the paper.

We observe outwardly rotating spiral waves filling in the space, as shown in Fig. 3(A) when the proper parameters are chosen. Figure 3(A) shows a series of snapshots of a well-developed single spiral spontaneously formed in system (2). The spiral is initiated on a 600×600 grid by the cross-field protocol and zero boundary conditions have been employed for simulations in the two dimensions. From the Fig. 3(A) we can see that the well-developed spiral waves are formed firstly by the evolution. Inside the domain, new waves emerge, but are evolved by the spiral waves growing from the center. The spiral waves can steadily grow and finally prevail over the whole domain. Fig. 3(B) show that the spiral waves first break up far away from the centre and eventually relatively large spiral fragments are surrounded by a ‘turbulent’ bath remain. The size of the surviving part of the spiral does not shrink if d_h is further decreasing until finally d_h equals to 0, on contrary, the spiral in the center grows more rapidly towards the outside (see Fig. 3(C)). Figure 3(D) is the time sequences (arbitrary units) of the variables p and h at an arbitrary spatial point, from which we can see that the spiral waves are caused by the accepted as “phase waves” with substantially group velocity, phase velocity and sinusoidal oscillation rather than the relaxational oscillation with large amplitude.

Furthermore, we know that the basic arguments in spiral stability analysis can be carried out by reducing the system to one spatial dimension [21, 22]. Here we show the essential properties of the spiral breakup resulting

from the numerical simulation and omit the detailed procedure. Breakup occurs first far away from the core (the source of waves). The spiral wave breaks towards the core until it gets to some constant distance and then the surviving part of the spiral wave stays stable. These minimum stable wavelengths are called λ_{min} . So the one-parameter family may be described by a dispersion curve $\lambda(d_h)$ (see Fig. 2). The minimum stable wavelength λ_{min} of the spiral wave in Fig. 2 come from the simulation in two dimensional space. The results of Fig. 2 can be interpreted as follows: the minimum stable wavelengths are increasing with respect to the d_h .

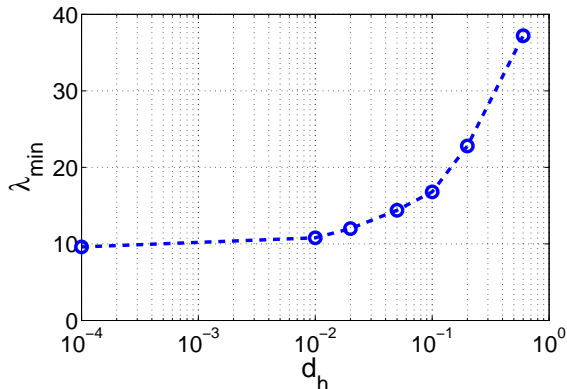


FIG. 2: Dependence of the wavelength λ_{min} on the parameter d_h for the system (2) with $r = 5.0$, $a = 5.0$, $b = 5.0$, $m = 0.6$, $d_p = 0.05$, and $n = 0.4$. Note the log scale for d_h .

We have investigated a plankton ecological system within two dimension space and found that its spatial patterns exhibit spiral waves, spatial chaos patterns, and moreover, the scenario of the spatial chaos patterns obtaining from the far-field breakup is reported. The reason causing this phenomenon can be illuminated theoretically by the M. Bär and L. Brusch study in Ref. [21, 22]. The far-field breakup can be verified in field observation and is useful to understand the population dynamics of oceanic ecological systems. So that, plankton plays an important role on the ecology of the ocean and the climate, because of their participation in the global carbon and nitrogen cycle at the base of the food chain. From the review [30], a recently developed ecosystem model incorporates different phytoplankton functional groups and their competition for light and multiple nutrients. Simulations of those model at specific sites to explore future scenarios suggest that global environmental change, including global-warming-induced changes, will alter phytoplankton community structure and hence alter global biogeochemical cycles [31]. The coupling of spatial ecosystem model to global climate raises again a series of open questions on model complexity and relevant spatial scales. So the study of spatial model with large-scale is more important in the ecological system. Basing on our numerical simulation on the spatial model, we can draft that the oceanic ecological systems show permanent spiral waves

and spatial chaos in large-scale over a range of parameter values d_h , and also periodically sustained plankton blooms in the local area. The spatial chaos patterns demonstrate the perspective observation of the Fig. 3 in Ref. [30].

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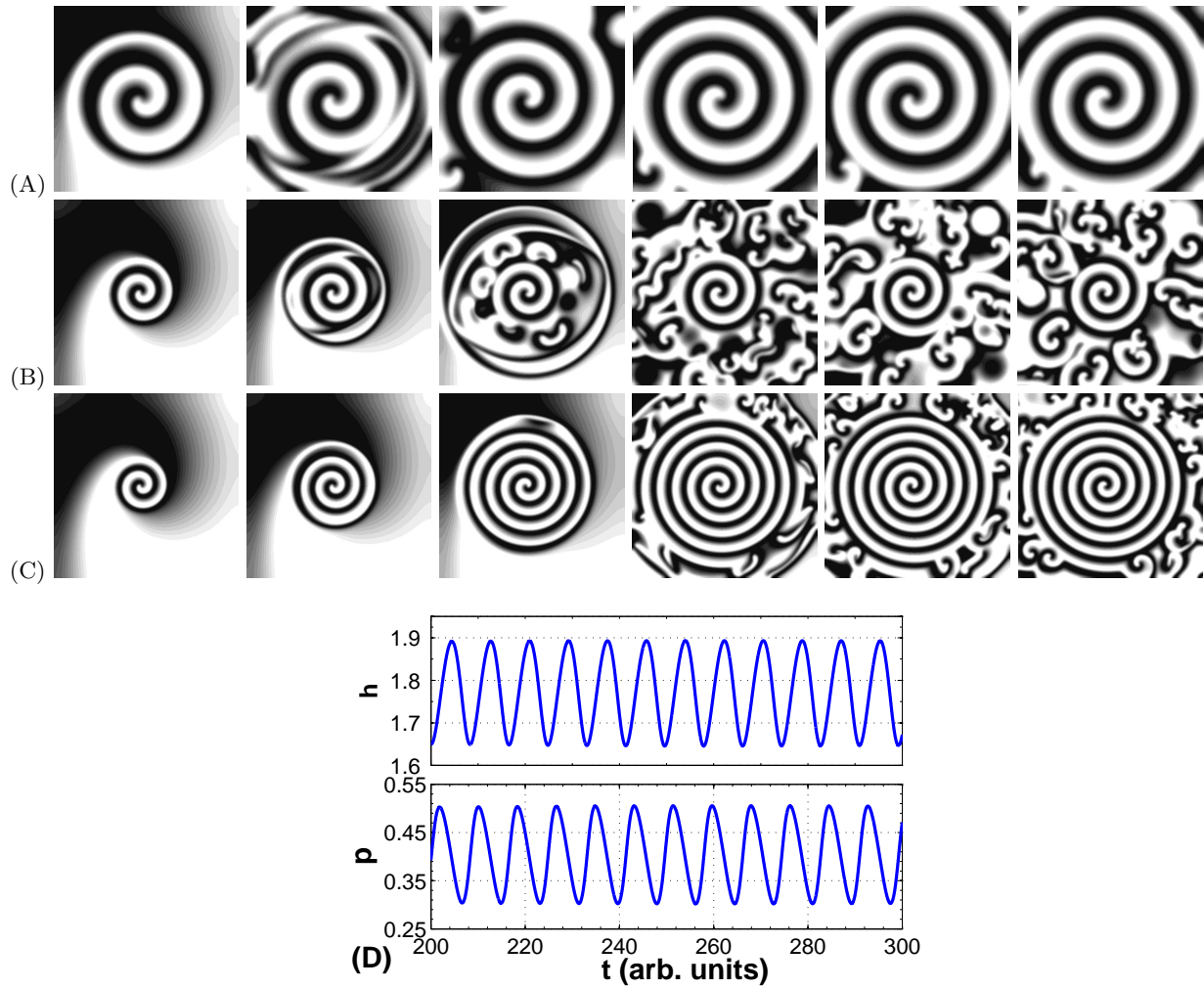


FIG. 3: Well developed spiral waves and some properties of them. The figures show simulations of the system (2) with $r = 5$, $a = 5$, $b = 5$, $m = 0.6$, $n = 0.4$, $d_p = 0.05$, and $f = 0.3$. (A) Well developed spiral waves shown at subsequent snapshot in time, $d_h = 0.2$. (B) Far-field breakup of the spiral waves shown at subsequent snapshot in time, $d_h = 0.02$. (C) Far-field breakup of the spiral waves shown at subsequent snapshot in time, $d_h = 0$. The white (black) areas correspond to maximum (minimum) values of p [Additional movie format available from the Web]. (D) Oscillations of the variable p and h at an arbitrary spatial point for both scenarios. Each figure is ran the long time until it spatial patterns are unchange.

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