Resonance and frequency-locking phenomena in spatially extended phytoplankton–zooplankton system with additive noise and periodic forces

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Abstract. It is known that natural systems are undeniably subject to random fluctuations, arising from either environmental variability or internal effects. In this paper, we present a spatial version of the phytoplankton–zooplankton model that includes some important factors such as external periodic forces, noise, and diffusion processes. The spatially extended phytoplankton–zooplankton system is from the original study by Scheffer (Scheffer 1991 Oikos \textbf{62} 271). Our results show that the spatially extended system exhibits a resonant pattern and frequency-locking phenomena. The system also shows that the noise and the external periodic forces play a constructive role in the Scheffer’s model: (i) the noise can enhance the oscillation of phytoplankton species’ density and form large clusters in space when the noise intensity is within a certain interval; (ii) the external periodic forces can induce 4:1 and 1:1 frequency-locking and spatially homogeneous oscillation phenomena to appear; and (iii) resonant patterns are observed in the system when the spatial noises and external periodic forces are both turned on. Moreover, we find that the 4:1 frequency locking transforms into 1:1 frequency locking when the noise intensity is increased. In addition to elucidating our results outside the domain of Turing instability, we provide further analysis of linear stability with the help of numerical calculation using

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the Maple software. Significantly, oscillations are enhanced in the system when the noise term is present. These results indicate that the oceanic plankton bloom may be partly due to interplay between the stochastic factors and external forces instead of deterministic factors. These results also may help us to understand the effects arising from the undeniable susceptibility to random fluctuations in oceanic plankton bloom.

Keywords: stochastic processes (theory), pattern formation (theory), population dynamics (theory), stochastic processes

1. Introduction

Many mechanisms of the spatio-temporal variability of natural plankton populations are not known yet. Pronounced physical patterns, such as thermoclines, upwelling, fronts, and eddies, often set the frame for the biological process. While many parameters and variables can be learned from standard oceanographic measurements of temperature, salinity, nutrients, and biomass concentrations of phytoplankton and zooplankton, now new technologies such as remote sensing are being developed for observing the ecosystem. Measurements of the underwater light field are made with state-of-the-art instruments and used to calculate concentrations of phytoplankton biomass, such as chlorophyll, as well as other forms of organic matter. More recently, satellite remote sensing and detailed numerical integration have identified some spatial patterns including filaments, irregular patches, sharp gradients, and other complex structures involving a wide range of spatial scales and timescales by utilizing the species’ concentration [1]–[3]. Figure 1 shows two pictures deriving from the field observation by satellite remote sensing, where color gives us very useful information and ideas about the changes of chlorophyll concentrations in two-dimensional space. More pictures of the spatial patterns of phytoplankton can be obtained from the website http://oceancolor.gsfc.nasa.gov, such as stripe-like, spotted-like, clockwise-rotating (or counterclockwise-rotating) spiral waves, and spatial chaotic

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Figure 1. These satellite images are the field observation of the phytoplankton blooms in the Malvinas current region. The enhanced natural color images show actual differences in water color while the pseudo-color image shows chlorophyll concentration. The images are taken from http://oceancolor.gsfc.nasa.gov, with permission from Campbell.

patterns. In particular, an observing system for monitoring the ecosystem is approached by posing five questions (see [1]): how is the ecosystem changing? What are the forcing factors causing it to change? How does the ecosystem respond to natural and human forces? Can we predict future changes? And what are the consequences for stakeholders in our region?

Learning from historical records and from our field observations in [4,5], one knows that the timing and magnitude of phytoplankton blooms vary significantly from interannual to longer timescales. For example, in some years, e.g. 2002, the spring bloom phytoplankton occurred in April, coinciding with vernal flowering on land, whereas in other years, e.g. 1999, the bloom occurred in February. Although there are only a handful of dynamic states that phytoplankton populations may exhibit, stable equilibrium, deterministic extinction, stable population oscillations, and irregular fluctuations, there is a long list of factors that may interact to determine the community dynamics, e.g. competition, predation, parasitism, mutualism, age, stage and genetic structure, spatial structure of the habitat, climate, and physical and chemical parameters. Thus, a key step in analyzing the community’s dynamics is to untangle these mixtures of
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interacting factors and to identify their necessity for the observed dynamics. In particular, from the experimental plankton communities [6] (rotifer-algal) one knows the following. First, the age structure of the predator populations is necessary to generate qualitatively correct predictions of population dynamics such as stability versus cycles. Second, the rapid evolution of populations, including the alga and rotifers, is regarded as a critical process occurring on the same timescale in the ecological dynamics, and it is learned that microcosms may not just serve as a means to check a model’s assumptions, but that the results of microcosm studies can lead to novel insights into the function of biological communities. From [7]–[9], we know that the inter-annual variation in zooplankton and phytoplankton species might be the result of changes in climate, and the photosynthetic phytoplankton growth strongly depends on the intensity of the light. Hence, these period factors are regarded as external periodic forces in the plankton systems. The variances of species evolving in time and space may be well understood.

Besides these periodic factors, there are many other stochastic factors causing phytoplankton–zooplankton blooms to transit extinction. For example, the effects arising from rivers’ pollution on the phytoplankton–zooplankton ecosystem is one of the ways that humans affect the marine ecosystem. Large rivers are major mechanisms for nutrient delivery to the ocean. Hence, the quality of river water affects freshwater ecosystems and oceanic food webs. Apart from this, the long term climatic variation also shows the stochastic factor of the ecological system (see [10] for a review on this point). In the phytoplankton–zooplankton systems, the random fluctuations also undeniably arise from either environmental variability or internal species. To quantify the relationship between fluctuations and species’ concentration with spatial degrees of freedom, the consideration of these fluctuations supposes we deal with noisy quantities whose variance might at times be a sizable fraction of their mean levels. For example, the birth and death processes of individuals are intrinsic fluctuations [11], which become especially pronounced when the number of individuals is small. The interaction between the oceanic zooplankton and fish, which are far from being uniformly distributed, also introduces randomness [12]. In addition, these processes can be regarded as parameters fluctuating irregularly with space and time. For example, phytoplankton production is affected by iron concentration, which can be elevated in surface water after rain [13]. These unavoidable fluctuations can also interact with the system’s nonlinearities to render counter-intuitive behavior, in which an increase in the noise level produces a more regular behavior [14]. Now, it is natural to ask what the spatio-temporal behaviors of the spatially extended plankton system are if these external periodic forces and the irregular fluctuation factors work on them. In particular, can the periodic oscillation still appear? In order to understand the stochastic force, we give a short introduction to noise application in physics and biology.

Recently, research interest has shifted to the effects of noise in a spatially extended system [14,15]. Well known examples in zero-dimensional (ODE) systems are noise-induced transition [16], stochastic resonance [17,18], enhanced spatial synchronization [19], and noise-sustained oscillations [20]–[22] (the reader can read an overview written by Sagués in [14]). More recently, effects of noise in spatially distributed systems, including noise-induced pattern formation [14,23,24], noise-induced fronts [25,26], etc, have been extensively studied by many communities. In these and other noise-related phenomena, multiplicative noise, which couples to the system state, plays a very special role. However, a prominent effect has been also found for additive noise.
Such influence has been observed in noise-induced pattern formation \cite{17, 24, 27--29}. A recent report \cite{30} demonstrated that additive noise which globally alternates between two different monostable excitable dynamics yields pattern formation. Meanwhile, in recent years several theoretical investigations have been done on noise-induced effects in population dynamics, see \cite{31--40}. Noise, such as from natural variability (measurement, Demographic, or environmental noise), is inevitably present in these types of systems, but its effects have not yet been addressed completely. In this paper, we report resonant patterns and frequency locked oscillations induced by additive noise and external forces in phytoplankton–zooplankton systems, and take into account the interplay among noise, external forces, and diffusion processes. In the following, we first give the spatially extended model and method we used, and then describe our results.

2. Model

From the recent perspective of Pascual \cite{41}, physical environments play an important role in the biota. If the climate sharply changes, the population abundance will change. In particular, the spatio-temporal dynamics of global population abundance, such as aggregated over the whole space \cite{42}, can be approximated by mean-field-type equations in which the functional forms specifying the growth rates and interactions have been modified as power functions. Moreover, the effect of interactions on local (or individual) scales can be represented implicitly by changing the form of the functions to describe interactions on global scales. We focus on the effects of periodic varying and stochastic fluctuation factors on the spatially extended phytoplankton and zooplankton model. Following Scheffer’s minimal approach \cite{43} and the previous analysis \cite{9, 44--46}, we study a two-variable phytoplankton and zooplankton spatial model involving time-periodic forces and a fluctuation term to describe the influence of spatial noise on pattern formation. It is worth noting that the emergence of noisy patterns such as those studied here is a feature shared across disciplines by many complex systems characterized by their out-of-equilibrium nature and nonlinear interactions. The more recent results show that, in the continuum limit, the stochastic partial differential equations (SPDEs) with additive noise can replace interaction among microscopic individuals including agents’ mobility \cite{47--49}.

In the absence of noise and force terms, the original spatially extended model is written as

\begin{align}
\frac{\partial P}{\partial t} &= RP \left( 1 - \frac{P}{K} \right) - \frac{A_1 C_1 P}{C_2 + P} H + D_p \nabla^2 P, \\
\frac{\partial H}{\partial t} &= \frac{C_1 P}{C_2 + P} H - M H - F \frac{H^2}{C_3^2 + H^2} + D_h \nabla^2 H,
\end{align}

where $P$ is phytoplankton biomass, $H$ is zooplankton biomass, and $D_p$ and $D_h$ are the diffusion coefficients of phytoplankton and zooplankton, respectively. The parameters $R$, $K$, $M$, and $1/A_1$ denote the intrinsic growth rate, carrying capacity of phytoplankton, death rate, and yield coefficient of phytoplankton to zooplankton. $F$ is the rate of zooplankton biomass consumed by fish per unit volume of water per day (average predation rate times the density of fish). The constants $C_1$, $C_2$, and $C_3$ parametrize the saturating functional response. When the noise and force terms are added to the right-hand side of all equations in equation (1), it is simpler to work with equation (1)
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that been rescaled to dimensionless form via
\[ t' = R_0 t, \quad r = \frac{R}{R_0}, \quad a = \frac{C_1 K}{C_2 R_0}, \quad b = \frac{K}{C_2}, \quad m = \frac{M}{R_0}, \]
\[ n = \frac{C_3 A_1}{K}, \quad d_p = \frac{k^2 D_p}{L R_0}, \quad d_h = \frac{k^2 D_h}{L R_0}, \quad f = \frac{F A_1}{C_3 R_0}, \]
and \( t \) is used to represent \( t' \), which leads to the dimensionless SPDE system as follows:\(^4\):
\[ \frac{\partial p}{\partial t} = r p(1 - p) - \frac{a p}{1 + b p} h + A \sin(\omega t) + d_p \nabla^2 p, \quad (2a) \]
\[ \frac{\partial h}{\partial t} = \frac{a p}{1 + b p} h - m h - f \frac{n h^2}{n^2 + h^2} + A \sin(\omega t) + \eta(r, t) + d_h \nabla^2 h. \quad (2b) \]
Here \( p(x, y, t) \) and \( h(x, y, t) \) are scalar fields representing the concentrations of phytoplankton species and zooplankton species in the two-dimensional space. It must also be kept in mind that the individuals of the population have not been at the same point in space at previous times, so they are a function of time. The periodic force is assumed to be sinusoidal with amplitude \( A \) and frequency \( \omega \). The periodic force is considered as an additive version for the reason that toxins produced by different phytoplankton species have a significant role in shaping the dynamical behavior of marine plankton ecosystems [50]. The zooplankton population tries to avoid the areas where the concentration of phytoplankton is very large. The reason may be either dense concentration or the effect of toxic substance released by phytoplankton, of course including the other factors as introduced in the previous section, such as human action and natural sharp changes—red tides and localized outbreaks occurring in coastal water and fronts [51]. Buskey and Stockwell [52] have shown in their field study that macro- and meso-zooplankton populations are reduced during the blooms of chrysophyte (Aureococcus anophagefferens). These factors are not directly correlated with species internal parameters, so that \( A \sin(\omega t) \) is added in the equation instead of \( A p(1 - p) \sin(\omega t) \).

Such consideration is meaningful in the biological systems (see [45, 53]). In equation (2), the stochastic factors are taken into account as the term, \( \eta(r, t) \), which is obtained in the continuum limit from the master equation (1) arising from microscopic interaction in the space [47]–[49] where the typical white noise will emerge. Recently, colored noise and white noise have both been used in describing ecological evolution [12, 39, 54, 55]. White noise is the limiting case of colored noise, so we consider the more general case—colored noise—in the present paper. Of course, due to the coupling, the noise in equation (2b) will have an influence on equation (2a) as well. Hence, we only need consider the noise presented in one of equations (2a) and (2b) (here, we consider noise presented in equation (2b)). The noise term \( \eta(r, t) \) is introduced additively in space and time, which is the Ornstein–Uhlenbech process [56]. The colored noise \( \eta(r, t) \), which is temporally correlated and white in space, satisfies
\[ \langle \eta(r, t)\eta(r', t') \rangle = \frac{\varepsilon}{\tau} \exp \left( -\frac{|t - t'|}{\tau} \right) \delta(r - r'), \quad (3) \]
where \( \tau \) controls the temporal correlation, and \( \varepsilon \) measures the noise intensity.

\(^4\) Here \( L \) and \( k \) denote the total length of the considered area and the number of nodes of the mesh for discretized space. The parameters \( r, a, b, m, n, d_p, d_h, \) and \( f \) refer to the previous works (see [44, 45] for details) on the dimensionless model (2) in the absence of periodic force and noise terms.

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In this work, we rely on numerical integration of the model of equation (2). We consider here spatio-temporal evolution of this system with space white noise and colored noise evolving in time when the system lies within the regime of self-sustained Hopf oscillation. Note that the explicit form of the noise term representing only the fluctuating recruitment rate (or death rate) has been studied by Malchow et al [11] and Blasius et al [39], in which the parameter \( m \) only is regarded as the noise form, i.e., \( m = m_0 + \xi(t); \xi(t) \) denotes Gaussian white noise. In the absence of external periodic forces and colored noise, Hopf instability occurs and spatially homogeneous oscillation arises when the parameter \( f \) is less than the critical value \( f_H = 0.3398 \) (see the appendix), whose value depends on the other parameters. Moreover, previous analysis and numerical simulations [57, 58] show that spiral wave structure exists in the two-dimensional space and the spatio-temporal chaos will emerge through its far-field breakup when the parameter \( f \) is within the mixed domain of the Hopf–Turing instability, but the parameters are outside the Turing instability domain in the present paper (see the appendix for a simple analysis). In fact, from a recent perspective, the 2:1 resonance phenomena on the spiral wave may appear when the system undergoes saddle-node or Hopf bifurcation [59]. In other words, the temporal period of the bifurcation patterns is twice the period of the primary spiral; i.e., the Hopf frequency \( \omega_H \) needs to be in a 2:1 resonance with the rotation frequency of the spiral wave. However, here we show that the system also exhibits spatio-temporal chaos patterns and the 4:1 and 1:1 resonances with the period of the external forces when fluctuations and periodic forces are considered. Except when it is explicitly pointed out, we take parameters \( r = 5, a = 5, b = 5, m = 0.6, n = 0.4, f = 0.3, d_p = 0.05 \), and \( d_h = 0.5 \) throughout this paper. These parameters were estimated by Medvinsky et al [9, 44, 45]. From these references, we know that these parameters are meaningful from the ecological point of view. The noise intensity \( \varepsilon \) and correlation time \( \tau \) are adjusted as control parameters. Without loss of generality, we have also tested the other slight modification parameter values \( d_p \) and \( d_h \) as well as \( f < f_H \), and similar qualitative results are still observed from the numerical integration results.

3. Results

Extensive testing was performed through numerical integration to describe model (2), and the results are shown in this section. In simulation, zero-flux boundary conditions are used and the time step is \( \Delta t = 0.05 \) time unit. The space step is \( \Delta x = \Delta y = 1 \) length unit and the grid sizes in the evolitional simulations are \( N \times N \) (\( N = 200 \)). The Fourier transform method is used for the deterministic part in equation (2). On the discrete square lattices, the stochastic partial differential equation (3) is integrated numerically by applying the Euler method. Several different discrete methods (simple Euler, Runge–Kutta, and Fourier transform) were checked, and the results indicate that the Fourier transform accurately approximates solutions of equation (2). On the other hand, the

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5 Blasius et al point out that the seasonal forcing and demographic noise (noncoupling with parameters) also play a key role in extended ecological systems, see [39, 40]. For example, the time series exhibited noise-induced chaos with the same uniform phase evolution and chaotic amplitude (UPCA) dynamics as the deterministic model in the simple foodweb model.

6 The frequency, \( \omega = 2\pi \times 10^{-1} \), of the forcing was chosen so that the intrinsic population cycle of the nutrient level comprised a year cycle.
Fourier method offers a speed advantage over other numerical methods. We find that on a PC the Fourier method runs about three to four times faster than the Euler integration using the same time step and space step. The code is implemented in Matlab 7.3 and the `fft2`, `fftshift`, `ifft2`, and `ifftshift` functions were used for the main numerical integration.

Although the noisy fluctuations may sometimes cause the variables \(p\) and \(h\) to be less than zero, it will lead to the diffusion–reaction system with cutoff effect at low densities when the species extinction is taken into account explicitly [60]. According to the spatially extended model (2), at each position in space, whenever the population densities fall below a certain prescribed value \(\varepsilon\) they are set to zero or a sufficiently small positive constant [60, 61]. From the biological point of view, in this paper we set them equal to 0.0001 when the variables change to negative. Note that we are not much concerned here with the ‘exact’ value of \(\varepsilon\), for the reason that an attempt to estimate the ‘exact’ value would hardly make any ecological sense in terms of a very schematic model (2). To compare with the numerical results under the different cases, we used the same initial conditions that are randomly perturbed (the perturbations are space independent) by homogeneous equilibrium \((p^*, h^*) = (0.3944, 1.7998)\), except when they are explicitly pointed out.

### 3.1. Dynamics in the presence of noise only

In the ecological systems, noise-sustained and noise-induced spatial pattern formations have been discussed in recent years [32]–[38]. For the convenience of discussion about the resonant pattern formation induced by additive noise and the external forces, here we firstly present a brief description of the effects arising from the fluctuations in the system (2). Our results show that the sole noise also plays a constructive role in model (2) by maintaining (or eliminating) the large spatial clusters (cf figures 3 and 4) and enhancing the aperiodic oscillation (see figure 5). Some typical snapshots of the spatial patterns at \(t = 300\) are presented in figure 2 and figures 3, 4 before and after the noise is added, respectively (see the captions of the figures). The ratio distribution of the two species is a key measurement in the ecological field. To characterize this measurement in the system (2), we introduce the parameter \(\theta\) \(\theta \in [-2\pi, 2\pi]\) and define it as follows:

\[
\theta = \text{arg}((p_{s,k} - p^*) + i(h_{s,k} - h^*)),
\]

where \(s, k = 1, 2, \ldots, N\). \(\theta\) indicates the relation between the two variables of the system, called the phase angle. Note that it also depicts the variance of the amplitude relevant to the two species in space, for the reason that its variables are the difference around the stable points, \(p^*\) and \(h^*\). Similarly, the following parameter, \(\mathcal{L}\), depicts the average amplitude for the system in space. However, we find that it is equivalent to the mean value of the variables in this system (cf figures 2, 7, 8, and 5), so we only use it in this section.

\[
\mathcal{L} = \ln \left( \frac{\sqrt{\sum (p_{s,k} - p^*)^2}}{N} \right),
\]

where \(s, k = 1, 2, \ldots, N\). The spatio-temporal chaotic spiral patterns appears when the noises are free (see figure 2), and large clusters can be recognized in space. \(\mathcal{L}\) or \(\langle p \rangle\) (\(\langle p \rangle\) denotes the spatial average of \(p\) at time \(t\)) oscillates with small fluctuations
Figure 2. Typical gray-scaled snapshots of spatio-temporal chaotic patterns at $t = 300$, when system (2) evolves in time without the noise term: (a), (b) the spatial patterns of $p$ and $h$, respectively; (c) the phase angle, $\theta$ (see the definition in the text); (d) the amplitude, $L$, evolves in time. (See [62].)

Figure 3. Typical gray-scaled snapshots of spatio-temporal chaotic patterns at $t = 300$, when the system (2) evolves in time with noise term. The meanings of the images correspond to figure 2, with the values of the parameters $\tau = 1$ and $\varepsilon = 0.001$. (See [62].)

(quasi-period)\(^7\), as shown in figures 2(d) (and figure 5), in which the abscissa is time and the ordinate is variable $L$. It is worth noting that the spatial correlation average is different from the time dependence of the correlation average. For the steady state, the

\(^7\) This steady state loses stability in a Hopf bifurcation to oscillations in the zero-dimensional mode as the parameter $f$ is decreased below a critical value $f_H = 0.3397$. 

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Figure 4. Typical gray-scaled snapshots of spatio-temporal chaotic patterns at $t = 300$. The same situation as figure 3 but $\varepsilon = 0.05$. (See [62].)

Figure 5. Direct comparison of the mean values of variable $p$ without and with noise term. The same situation as figures 2–4.

time dependence average can drop out, because of translational and rotational invariance for the spiral waves. The behavior of the system undergoes drastic changes when the noises are turned on (cf figures 2, 3, and 4). First, the large spatio-temporal chaotic clusters die out gradually with the increasing of noise intensity; second, the oscillations of $\mathcal{L}$ become more obvious when the noise intensity is within a certain region, but it stays at a fixed value again if the noise intensity is further increased. To summarize, compared with figures 2, 3, and 4, it should be noted that the noise plays a constructive role in the relation between phytoplankton and zooplankton in space.
3.2. Dynamics in the presence of the external forces only

From the previous analysis [8], it is known that the plankton system (2) has very complex dynamical behaviors such as the scenario of bifurcations and chaos when the spatial degree of freedom was not considered. However, we here consider the case where the parameter values are within the Hopf oscillation interval and the spatial degree of freedom is taken into account.

The parameter values that we took in previous section 2 give that the system is noise free, thus the spatially homogeneous oscillation does not respond to the external periodic force if the amplitude $A$ is below a threshold $A_c$, whose value depends on the external period $T_{in} = 2\pi/\omega$. Above the threshold, the system (2) produces oscillations about period $T_{out}$ with respect to the external period $T_{in}$; this phenomenon is called frequency locking or resonant response, i.e., when the system produces one spike within each of the $M = 1, 2, 3, \ldots$ periods of the external force, that is, $M:1$ resonant response. In the present paper, the output period $T_{out}$ is defined as follows: $T_i$ is the time interval between the $i$th spike and the $(i+1)$th spike. $q$ spikes are taken into account and their average value is $T_{out}$, where $T_{out} = (\sum_{i=1}^{q} T_i)/(q-1)$ [63].

Two types of frequency-locking phenomena are observed in the spatially extended model (2). They are 4:1 and 1:1 frequency locking. In figures 6(a) and (b), we have plotted the temporal evolution of the variable $p$ when the amplitude $A$ is above the threshold, where the 4:1 and 1:1 frequency lockings take place, respectively. In these cases, the spatially homogeneous oscillation patterns depend on the initial conditions, and two-phase patterns with a phase shift and separated by a stationary Ising front (in particular, for the initial conditions coming from [45], that is $p(x, y, 0) = p^*$ and $h(x, y, 0) = h^* + \epsilon x + \delta$; here $\epsilon$ and $\delta$ are parameters), or alternative homogeneous oscillations come out (see figure 6(c)). From the random initial conditions prepared by randomly perturbing around the homogeneous steady state $(p^*, h^*)$, we obtain 4:1 resonant homogeneous oscillations, such as an example shown in figure 6(c), which plots the space–time figure for the homogeneous patterns to compare with the external force, and illustrates that the patterns are well 4:1 frequency locked. Moreover, the 4:1 frequency locking was demonstrated with a power spectrum as shown in figure 10, i.e., $T_{out}:T_{in} = 2\pi/\omega':2\pi/\omega = 4:1$. Note that the green lines in figure 6 only denote the exact temporal period of the external forces rather than its values for comparison.

3.3. Dynamics under both noise and external forces

Now, we turn on the additive noise and periodic forces in the system (2). To check their effects on the system (2) within the 4:1 frequency-locking regimes, we adjust the noise intensity and correlation time. At the first series of simulations, when we adopt $\tau = 1.0$, and adjust the noise intensity $\varepsilon$, from our simulation results it is important to note that under the fixed noise intensity the colored noise (corresponding to the large $\tau$) is not necessary for the resonant pattern in our system, but it is the source of large cluster/aggregation. We also find that white noise\(^8\) can induce a resonant pattern to appear. Considering the influences of noise and spatial distribution on the system, we

\[^8\] Here, our white noise comes from the limiting case of colored noise, i.e., $\tau$ goes to zero and white noise is obtained. The resonant pattern remains when $\tau = 10^{-4}$. 

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Figure 6. Sequences of the mean concentration $\langle p \rangle$, noise free. (a) The 4:1 frequency-locking oscillation with the values of the parameters $A = 0.1$ and $\omega = 2\pi \times 10^{-1}$. (b) The 1:1 frequency-locking oscillation with the values of the parameters $A = 0.1$, but $\omega = \pi \times 10^{-1}$. (c) The space–time diagram (right panel) displays the time evolution of the patterns in the one-dimensional space. For comparison, the curve in the left panel shows the periodic external force. In (c), the left and right windows share the same ordinate, which is time. Note that the green lines only denote the exact temporal period of the external forces rather than its values for comparison.

performed the simulation starting at $\varepsilon = 0.001$, and then $\varepsilon$ is increased in small steps $\Delta \varepsilon = 0.001$ until the noise intensity is a large enough value. The noise drastically changes the previous scenarios in the system including the spatial patterns and frequency locking when the noise intensity is strong enough (see figure 7). First, the spatial patterns with homogeneous oscillation are replaced by the spatial heterogeneous oscillations. This means that the distribution of the species may appear in spatial patterns and its bloom is periodic in space when some fluctuations work on the system (see figure 7(a)). Second, the frequency locking (4:1) shifts into the other type of frequency locking (1:1) (see figure 7(b)).
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Figure 7. Spatial frequency-locking patterns and the time series of the mean value \(\langle p \rangle\) of the concentration \(p(x, y)\) with respect to different noise intensities \(\varepsilon\). (a) Gray-scaled snapshots of spatial frequency-locking patterns with different noise intensities \(\varepsilon\), where the noise intensity is 0.001 and 0.05 for the middle column and the right-hand column (see [62]). (b) The change of the frequency locking with respect to the different noise intensities. Parameters are the same as figure 6(a) except \(\varepsilon\). (c) The space–time diagram corresponding to figure 7(a)(right).
From our numerical results (cf figure 7), one could conclude that homogeneous oscillations depend on the noise intensity. The oscillations are only slightly perturbed, or not affected when the noise intensity $\varepsilon$ is small. As $\varepsilon$ is increased, the homogeneous oscillating patterns lose their stability and associate with the frequency locking change. Figure 7(a) (middle column) shows that an oscillating two-phase pattern with local spotted patterns will appear at $\varepsilon = 0.001$. When the noise intensity is further increased, the spotted patterns show aggregation behavior, and become large clusters in space. Figure 7(a) (right-hand column) shows a clear spatial oscillation pattern with large clusters will appear at $\varepsilon = 0.050$. The stochastic resonance pattern is confirmed by the space–time diagram (figure 7(c)). In figure 7(b) we have plotted the temporal evolution of the variable $\langle p \rangle$ when the noise intensity is taken as different values. It is interesting to realize that the resonant patterns and the frequency locking do not alter on increasing the noise intensity within a large interval (e.g. 0.0005 to 0.001; 0.05 to 0.10). The variable $\langle h \rangle$ also exhibits similar characteristics in the model. Note that we do not observe that the demographic noise induces UPCA-like oscillations to appear in system (2) for parameter regimes where the model was parametrized to give limit cycle behavior in the absence of noise and periodic forcing (see the appendix and the bifurcation diagram in [58]).

In order to elucidate the evolutional processes of the spatial structure, we have depicted typical spatio-temporal patterns of the system (2) within one period $T_{out}$, as shown in figure 8. The other periods also exhibit similar characteristics.

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Note here that UPCA refers to as oscillation with uniform phase evolution, yet chaotic amplitudes.
Figure 9. Phase diagram in $\epsilon$–$\tau$ parameter space, with $A = 0.1$ and $\omega = 2\pi \times 10^{-1}$. There are two states: 4:1 (region B) and 1:1 (region A). The solid line is a least-square fit of the circle data.

The previous figures 6 and 7 exhibit an aspect of the frequency locking and resonant pattern which has received considerable attention in recent years, namely, the response of the system to a periodic force may be enhanced by the presence of noise [14, 17, 22, 29, 64, 65].

The role of temporal correlation $\tau$ of the colored noise is also significant including its intensity in inducing and controlling the spatial pattern formation and transition of the resonant patterns. Now, it is natural to ask what the consequence of the temporal correlation of the colored noise is, in particular, the phase diagram of the $\epsilon – \tau$ parameter space. In order to well understand the phase transition by the influence of temporal correlation $\tau$, we performed a series of simulations, fixing $\tau$ and scanning the noise intensity, $\epsilon$, when the frequency locking evidently changes in the long term (here we run the time up to 5000) and recorded the data. Figure 9 summarizes the results from the numerical integration, in which regions A and B correspond to the 1:1 frequency locking and 4:1 frequency locking respectively. Figure 9 depicts the transition point of frequency locking shifting toward higher values of the noise intensity as the correlation time is increased; that is, $\tau$ softens the effect of the noise.

4. Conclusion and discussion

It is known that an external periodic force applied to a nonlinear pendulum can cause the pendulum to become entrained at a frequency which is rationally related to the applied frequency, a phenomenon known as frequency locking [66]. A recent theoretical analysis shows that an array of coupled nonlinear oscillators can exhibit spatial reorganization when they are subjected to external periodic forces [67]. In this paper, we present a spatial version of the phytoplankton–zooplankton model that includes some important factors such as external periodic forces, random fluctuations, and diffusion processes. The modified system is based on the original model by Scheffer [43, 44], but here it can exhibit frequency-locking phenomena and resonant patterns. Our results show that the noise and the external periodic forces play a constructive role in the Scheffer’s model: first, the noise can enhance the oscillation of the species’ density and form large clusters in space. Second, the external periodic forces can induce 4:1 and 1:1 frequency-locking and
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Figure 10. The corresponding power spectrum for the density of variable $p$ as a function of its frequency with the parameter values $\omega = 2\pi \times 10^{-1}$ and $\varepsilon = 0.001$ (the same as figure 6(a)). Note that the period was normalized to units so that $T_{\text{out}} = 1/\omega'$. It is worth emphasizing that the frequency lockings and resonant patterns only appear when noise and external forces are present in the model (2). We here consider the cases when the unforced system lies outside the Turing instability (see the appendix for details). The typical power spectrum $P(\omega')$ related to the density of the phytoplankton for the oscillations within 4:1 frequency locking is analyzed, as shown in figure 10. The power spectrum related to the density of zooplankton (not shown here) is similar. The presence of a prominent and well defined peak in the power spectrum of figure 10 at a nonzero frequency characterizes oscillating behavior. From figure 10, one could see that the oscillation behavior relates to the external periodic forces and the natural frequency, $\omega_H$ (see the appendix), of the system. Significantly, oscillations are enhanced in the system when a single noise term is present. These results indicate that the oceanic plankton bloom may be partly due to the interplay between external forces and stochastic factors instead of deterministic factors. Our results may also help us to understand the effects arising from the undeniable susceptibility to random fluctuations in oceanic plankton bloom.

In this paper, we study the effects of noise and external forces on a spatially extended phytoplankton–zooplankton system in static media (with the advection term not prominent). However, in the oceanic ecological systems the biological processes among the species are in a fluid environment, such as turbulent flows or chaotic advection. Recently, a few authors have considered the mixing of the flow and diffusion processes using a well known standard model of chaotic advection [3, 22], [68]–[73] in excitable media; in particular, Reigada et al [74] found that plankton blooms can also be induced by turbulent

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flows. So, a further study in our work will analyze the effects arising from the mixing of advection, diffusion, external forces and noise. It is also interesting to apply the problem of oceanic plankton bloom and the spatial structure observed in the field as a introduction in section 1.

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Appendix. Stability analysis with the help of Maple

This appendix is devoted to the numerical analysis of the unforced system (A.1).

\[
\frac{dp}{dt} = rp(1 - p) - \frac{ap}{1 + bp}h , \quad (A.1a)
\]

\[
\frac{dh}{dt} = \frac{ap}{1 + bp}h - mh - f \frac{nh^2}{n^2 + h^2} . \quad (A.1b)
\]

Setting the left-hand sides of system (A.1) to zero, we obtain

\[
g_1(p, h) = rp(1 - p) - \frac{ap}{1 + bp}h , \quad (A.2)
\]

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

Equations (A.2) and (A.3) give a unique interior equilibrium \((p^*, h^*)\), when parameter \(f\) is less than 0.445.

Now we consider the stability of this positive equilibrium. The Jacobian matrix at the positive equilibrium \((p^*, h^*)\) is

\[
J = \begin{pmatrix}
\frac{\partial g_1}{\partial p}(p^*, h^*) & \frac{\partial g_1}{\partial h}(p^*, h^*) \\
\frac{\partial g_2}{\partial p}(p^*, h^*) & \frac{\partial g_2}{\partial h}(p^*, h^*)
\end{pmatrix} . \quad (A.4)
\]

Its eigenvalues, \(\lambda_{1,2}\), were listed in table A.1 with the different parameter values \(f\). The first type of instability is associated with a Hopf bifurcation in the spatially uniform
system. This instability will appear at the threshold \( f_H \) and oscillate homogeneously with the natural frequency \( \omega_H = \text{Im}(\lambda_{1,2}) \). From table A.1, one could see that the natural frequency is equal to 0.8221 if \( f = 0.30 \).

Now we consider the spatial inhomogeneous perturbation by using the techniques of Koch and Meinhardt [75].

\[
\delta p = \delta p_0 \exp(\lambda' t + i k r), \quad \delta h = \delta h_0 \exp(\lambda' t + i k r),
\]

with wavenumber vector \( k = (k_x, k_y) \), \( |\delta p_0|, |\delta h_0| \ll 1 \) and imaginary unit \( i^2 = -1 \). Due to the zero-flux boundary conditions, \( k_x \) and \( k_y \) take only discrete values

\[
k^n_x = k^n_y = n \pi / L, \quad n = 0, 1, 2, \ldots,
\]

where \( L \) is the size of the space. Each \( k^n \) is associated with a ‘frequency’ \( \omega_n \), which can be a complex number. The functions \( \omega_n(k^n) \) are found by substituting expression (A.5) into the following equation:

\[
\frac{\partial p}{\partial t} = rp(1 - p) - \frac{ap}{1 + bp} h + d_p \nabla^2 p, \tag{A.7a}
\]

\[
\frac{\partial h}{\partial t} = \frac{ap}{1 + bp} h - mh - f \frac{n h^2}{n^2 + h^2} + d_h \nabla^2 h. \tag{A.7b}
\]

Retaining terms up to first order in \( \delta p \) and \( \delta h \), we get the linearized equation:

\[
J' \begin{bmatrix} \delta p \\ \delta h \end{bmatrix} = 0, \tag{A.8}
\]

with

\[
J' = \begin{bmatrix}
\frac{\partial g_1}{\partial p} (p^*, h^*) - d_p (k^n)^2 - \lambda' & \frac{\partial g_2}{\partial h} (p^*, h^*) \\
\frac{\partial g_2}{\partial p} (p^*, h^*) & \frac{\partial g_2}{\partial h} (p^*, h^*) - d_h (k^n)^2 - \lambda'
\end{bmatrix}.
\]

The perturbation amplitudes \( \delta p_0 \) and \( \delta h_0 \) can be different from zero if and only if \( \det J' \neq 0 \).

The Turing instability is expected to occur for finite \( k^n > 0 \), and at least one of the real parts becoming greater than zero. If \( f \) is taken as a control parameter, the critical point is reached if the determinant \( J' \) has a pure imaginary eigenvalue, i.e. \( f = f_T \), \( \text{Re}(\lambda'_{1,2}) = 0 \), and for the critical wavenumber can be written as

\[
(k^n)^2 = \frac{d_h J_{11} + d_p J_{22}}{2d_p d_h}, \tag{A.10}
\]

\( J_{11} \) and \( J_{22} \) are the elements of the matrix \( J \).

Table A.2 lists the eigenvalues of the Jacobian matrix (A.9) and the critical wavenumber \( k^n_c \), from which one can see that our simulation is outside the Turing instability regime when \( f = 0.30 \).

### Table A.1. The eigenvalues of the Jacobian matrix (A.4).

| \( f \) | 0.30 | 0.3397 | 0.3398 | 0.3399 |
| --- | --- | --- | --- | --- |
| \( \lambda_{1,2} \) | 0.0473 ± 0.8221i | 0.0001 ± 0.8040i | 0.0000 ± 0.8039i | −0.0001 ± 0.8039i |
The Maple program is available on request.

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Table A.2. The eigenvalues of the Jacobian matrix (A.9).

| $f$  | 0.30 | 0.3124 | 0.3125 |
|------|------|--------|--------|
| $\lambda_1$ | -0.0704 ± 0.8177i | -0.0003 ± 0.8174i | 0.0003 ± 0.8174i |
| $k_0$ | 0.6539 | 0.3480 | 0.3444 |

Spatio-temporal stochastic resonance in excitable media

The Maple program is available on request.

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