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A Study on the Effects of Riesz Fractional Diffusion on Pattern Formation in a Toxic-Phytoplankton–Zooplankton Model

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Abstract

In this paper, we investigate Turing instability and spatiotemporal pattern formation in a toxic-phytoplankton–zooplankton model incorporating Riesz fractional diffusion. By replacing classical Laplacians with fractional-order operators $(-\Delta)^{\phi/2}$ and $(-\Delta)^{\psi/2}$, we establish a framework to capture species-specific anomalous diffusion in aquatic ecosystems. Theoretical analysis demonstrates that the fractional orders significantly modulate the Turing bifurcation threshold and the range of unstable modes. Numerical simulations, implemented via a DCT-based fractional finite difference scheme, reveal that: (1) fractional diffusion triggers pattern formation below the classical critical threshold, generating complex mixed structures unattainable in integer-order models; (2) the two fractional orders exert opposing influences on pattern morphology—decreasing the phytoplankton order ϕ promotes a transition from stripes to hexagonal spots. Our results suggest that anomalous diffusion is a key mechanism for ecological pattern selection, providing new insights into the spatiotemporal complexity of plankton populations in heterogeneous environments.

Keywords: Riesz fractional diffusion; spatiotemporal pattern; Turing bifurcation; cross diffusion; anomalous diffusion; plankton dynamics

MSC: 35B32

1. Introduction

Spatiotemporal pattern formation is a ubiquitous phenomenon in natural systems, spanning from complex chemical reactions to intricate ecological dynamics [1–4]. In aquatic ecosystems, the spatial distribution of plankton populations often manifests as organized patches, which are recognized as crucial determinants for species coexistence and the onset of harmful algal blooms [5]. The pioneering work of Turing (1952) revealed that diffusion can paradoxically destabilize a homogeneous steady state when coupled with appropriate reaction kinetics [1]. Recent advances have further deepened our understanding, uncovering complex dynamics such as nonlinear pattern selection and spatial chaos within diverse ecological landscapes [6].

Real-world aquatic environments are often characterized by turbulence where the traditional Brownian motion assumption is frequently violated. Consequently, fractional-order partial differential equations (PDEs) have emerged as a robust framework for modeling anomalous diffusion and non-local interactions [7–13]. Unlike integer-order PDEs, fractional operators effectively capture long-range spatial correlations and scale-invariant properties intrinsic to biological systems. While time-fractional PDEs model history-dependent



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processes [11], spatial fractional PDEs involving the Riesz fractional Laplacian $(-\Delta)^{\alpha/2}$ have gained prominence for describing super-diffusive transport in turbulent media [14,15]. Recent research suggests that spatial fractional diffusion can fundamentally reshape bifurcation conditions and significantly modulate the morphology of spatial structures.

In the context of interacting populations, the coupling of fractional calculus with cross-diffusion mechanisms has recently attracted attention. Yao et al. [16] demonstrated that introducing cross-fractional diffusion into a predator–prey model with mutual interference can induce Turing patterns in regimes that otherwise exhibit only bistability. Similarly, Iqbal and Wu [17] utilized weakly nonlinear analysis to classify pattern morphologies, such as squares and spots, in a fractional cross-diffusion system with a Beddington–DeAngelis functional response. However, these studies primarily focus on standard predator–prey interactions. While Han and Dai [18] investigated cross-diffusion induced instability in a toxic-phytoplankton–zooplankton (TPP-Z) model, their study was confined to the integer-order framework. To date, the combined effects of Riesz fractional diffusion and cross-diffusion on the complex antagonistic dynamics of toxic-phytoplankton–zooplankton systems remain underexplored, particularly regarding how species-specific anomalous diffusion rates modulate pattern selection.

This study builds upon the rich legacy of Turing analysis, focusing specifically on the TPP-Z model. This model describes antagonistic interactions where phytoplankton produces toxins that inhibit predation. The original model incorporates mechanisms such as the Allee effect and Holling type IV functional responses [19,20]. Furthermore, the essential role of cross-diffusion in predator–prey spatial coupling has been explored to explain complex patterns beyond classical Fickian diffusion [2,21–25]. Recent work on fractional-order ecological models has extended these concepts to multi-species interactions, providing new insights into the role of anomalous diffusion in complex food webs [26,27]. The original integer-order TPP-Z system is governed by:

$$\frac{\partial P}{\partial t} = rP \left(1 - \frac{P}{K}\right) (P - m) - \frac{\alpha PZ}{c + eP^2} + a_1 \nabla^2 P, \quad (1a)$$

$$\frac{\partial Z}{\partial t} = \frac{(\beta - \theta)PZ}{c + eP^2} - dZ + \nabla^2 [(a_2 + bP)Z], \quad (1b)$$

where $P(x, t)$ and $Z(x, t)$ represent the population densities of phytoplankton and zooplankton, respectively. The ecological parameters include the growth rate r , carrying capacity K , Allee threshold m , predation rate α , functional response coefficients c and e , conversion efficiency β , toxin production rate θ , and mortality d . a_1 and a_2 denote self-diffusion, while b represents the cross-diffusion coefficient which captures the zooplankton's behavioral response to phytoplankton density. To better reflect the anomalous transport observed in turbulent aquatic environments, we extend this model by replacing the classical Laplacian operators with Riesz fractional Laplacians of potentially different orders for each species. The resulting fractional-order system is:

$$\frac{\partial P}{\partial t} = rP \left(1 - \frac{P}{K}\right) (P - m) - \frac{\alpha PZ}{c + eP^2} - a_1 (-\Delta)^{\phi/2} P, \quad (2a)$$

$$\frac{\partial Z}{\partial t} = \frac{(\beta - \theta)PZ}{c + eP^2} - dZ - (-\Delta)^{\psi/2} [(a_2 + bP)Z], \quad (2b)$$

where $(-\Delta)^{\phi/2}$ and $(-\Delta)^{\psi/2}$ are the Riesz operators of order $\phi, \psi \in (1, 2]$. The Riesz fractional Laplacian operator $(-\Delta)^{\gamma/2}$ for $\gamma \in (1, 2]$ is rigorously defined as a pseudo-differential operator via its Fourier transform:

$$\mathcal{F} \left[(-\Delta)^{\gamma/2} u(\mathbf{x}) \right] (\mathbf{k}) = |\mathbf{k}|^\gamma \hat{u}(\mathbf{k}), \quad (3)$$

where $\mathbf{k}$ denotes the wavevector and $\hat{u}(\mathbf{k})$ is the Fourier transform of $u(\mathbf{x})$. Equivalently, in n -dimensional space, the Riesz fractional operator can be expressed in terms of a singular integral:

$$(-\Delta)^{\gamma/2}u(\mathbf{x}) = C_{n,\gamma} \int_{\mathbb{R}^n} \frac{u(\mathbf{x}) - u(\mathbf{y})}{|\mathbf{x} - \mathbf{y}|^{n+\gamma}} d\mathbf{y}, \quad (4)$$

where $C_{n,\gamma}$ is a normalization constant. This integral representation highlights the non-local interaction mechanism, where the state at point $\mathbf{x}$ depends on the long-range spatial correlations across the entire domain. This species-specific fractional framework allows us to investigate how the interplay between different anomalous diffusion rates—reflecting the passive drifting of phytoplankton versus the active, non-local movement of zooplankton—affects pattern selection and ecological stability, providing a more nuanced understanding of real-world plankton dynamics.

The structure of this paper is as follows: Section 2 provides a rigorous theoretical analysis, deriving the conditions for Turing instability and exploring how the fractional orders ϕ and ψ modulate the critical wavenumber and the range of unstable modes. Section 3 introduces our numerical methodology, utilizing a fractional finite difference scheme coupled with the Discrete Cosine Transform (DCT-II) for efficient simulation under Neumann boundary conditions, and discusses the resulting pattern morphologies. Section 4 summarizes our findings and discusses their broader biological implications and potential for future ecological research.

2. Theoretical Analysis

2.1. Equilibrium

The equilibrium points of system (2) are identical to those of the original system (1), as they are determined solely by the reaction terms. The system admits the following equilibrium points:

1. Trivial equilibrium: $E_0 = (0, 0)$
2. Boundary equilibria: $E_{10} = (K, 0)$ and $E_{20} = (m, 0)$ (the latter exists only for strong Allee effect, $m > 0$)
3. Positive coexistence equilibria: $E_1^* = (P_1^*, Z_1^*)$ and potentially $E_2^* = (P_2^*, Z_2^*)$, where P_i^* satisfies

$$edP^2 - (\beta - \theta)P + cd = 0, \quad (5)$$

$$\text{with } m < P_i^* < K, \text{ and } Z_i^* = \frac{r(K - P_i^*)(P_i^* - m)(c + eP_i^{*2})}{\alpha K}.$$

Assuming $(H_1) : \mathcal{R}_0 > 2\sqrt{ce}$ is satisfied, the positive equilibrium E_1^* exists if:

$$m < \frac{\mathcal{R}_0}{2e} - \sqrt{\frac{\mathcal{R}_0^2}{4e^2} - \frac{c}{e}} < K < \frac{\mathcal{R}_0}{2e} + \sqrt{\frac{\mathcal{R}_0^2}{4e^2} - \frac{c}{e}}, \quad (6)$$

where $\mathcal{R}_0 = \frac{\beta - \theta}{d}$, $P_1^* = \frac{\mathcal{R}_0}{2e} - \sqrt{\frac{\mathcal{R}_0^2}{4e^2} - \frac{c}{e}}$ and $Z_1^* = \frac{r(K - P_1^*)(P_1^* - m)(c + eP_1^{*2})}{\alpha K}$. Let $\mathcal{R}_1 = K - \frac{\mathcal{R}_0}{2e} - \sqrt{\frac{\mathcal{R}_0^2}{4e^2} - \frac{c}{e}}$ and $\mathcal{R}_2 = \frac{\mathcal{R}_0}{2e} - \sqrt{\frac{\mathcal{R}_0^2}{4e^2} - \frac{c}{e}} - m$. The equilibrium E_1^* is locally asymptotically stable if: $P_1^* > \frac{K+m}{2}$ (away from Allee threshold) and $\frac{\mathcal{R}_0}{\mathcal{R}_2} - \frac{\mathcal{R}_0}{\mathcal{R}_1} + 2e < 0$ (ensures $\text{tr}(\mathcal{J}_{E_1^*}) < 0$). These conditions ensure both $\text{tr}(\mathcal{J}_{E_1^*}) < 0$ and $\det(\mathcal{J}_{E_1^*}) > 0$.

2.2. Turing Bifurcation Analysis with Fractional Diffusion

We now investigate the conditions under which the spatially homogeneous equilibrium E_1^* becomes unstable to spatially inhomogeneous perturbations when fractional diffusion is present.

Consider perturbations of the form:

$$\begin{pmatrix} P \\ Z \end{pmatrix} = \begin{pmatrix} P_1^* \\ Z_1^* \end{pmatrix} + \begin{pmatrix} \hat{p} \\ \hat{z} \end{pmatrix} e^{i\mathbf{k} \cdot \mathbf{r} + \lambda t}, \quad (7)$$

where $\hat{p}$ and $\hat{z}$ are the amplitudes of small perturbations, $i = \sqrt{-1}$ is the imaginary unit, $\mathbf{k}$ is the wavevector with magnitude $k = |\mathbf{k}|$, $\mathbf{r}$ denotes the spatial position vector, and λ is the eigenvalue (growth rate) determining the temporal evolution of the perturbation. In Fourier space, the linearized system becomes:

$$\lambda \begin{pmatrix} \hat{p} \\ \hat{z} \end{pmatrix} = M(k) \begin{pmatrix} \hat{p} \\ \hat{z} \end{pmatrix}, \quad (8)$$

where the dispersion matrix is:

$$M(k) = \begin{pmatrix} \mathcal{J}_{11} - a_1 |k|^\phi & \mathcal{J}_{12} \\ \mathcal{J}_{21} - bZ_1^* |k|^\psi & -(a_2 + bP_1^*) |k|^\psi \end{pmatrix} \quad (9)$$

where $\mathcal{J}_{ij}$ are the elements of the Jacobian matrix evaluated at the equilibrium E^* :

$$\mathcal{J}_{11} = r \left[\left(1 - \frac{P^*}{K}\right)(P^* - m) - \frac{P^*(P^* - m)}{K} + P^* \left(1 - \frac{P^*}{K}\right) \right] - \frac{\alpha Z^*(c - eP^{*2})}{(c + eP^{*2})^2}, \quad (10a)$$

$$\mathcal{J}_{12} = -\alpha P^* / (c + eP^{*2}), \quad (10b)$$

$$\mathcal{J}_{21} = (\beta - \theta) Z^* (c - eP^{*2}) / (c + eP^{*2})^2, \quad (10c)$$

$$\mathcal{J}_{22} = (\beta - \theta) P^* / (c + eP^{*2}) - d = 0. \quad (10d)$$

The characteristic equation is:

$$\lambda^2 - \text{tr}(M(k))\lambda + \det(M(k)) = 0, \quad (11)$$

with

$$\text{tr}(M(k)) = \mathcal{J}_{11} - a_1 |k|^\phi - (a_2 + bP_1^*) |k|^\psi, \quad (12a)$$

$$\det(M(k)) = a_1(a_2 + bP_1^*) |k|^{\phi+\psi} + [\mathcal{J}_{12}bZ_1^* - \mathcal{J}_{11}(a_2 + bP_1^*)] |k|^\psi - \mathcal{J}_{12}\mathcal{J}_{21}. \quad (12b)$$

For Turing instability to occur, two conditions must be satisfied: (a) The homogeneous equilibrium is stable: $\text{tr}(M(0)) < 0$ and $\det(M(0)) > 0$; (b) There exists a wavenumber $k \neq 0$ such that $\det(M(k)) < 0$ or $\text{Re}(\lambda(k)) > 0$.

The critical point (b_c, k_c) satisfies the bifurcation conditions:

$$\det(M(k_c)) = 0, \quad \left. \frac{\partial \det(M(k))}{\partial k} \right|_{k=k_c} = 0. \quad (13)$$

To determine the critical wavenumber, we first simplify the determinant expression in Equation (12b). Let us define the auxiliary function $H(b)$ as:

$$H(b) = \mathcal{J}_{11}(a_2 + bP_1^*) - \mathcal{J}_{12}bZ_1^*. \quad (14)$$

With this notation, the coefficient of the $|k|^\psi$ term in Equation (12b) becomes $-H(b)$. Differentiating Equation (12b) with respect to k and applying the condition $\partial \det(M(k))/\partial k = 0$, we obtain:

$$(\phi + \psi)a_1(a_2 + b_c P_1^*)|k_c|^{\phi+\psi-1} - \psi H(b_c)|k_c|^{\psi-1} = 0. \quad (15)$$

Solving this equation for $|k_c|$ yields the expression for the critical wavenumber:

$$|k_c|^\phi = \frac{\psi H(b_c)}{(\phi + \psi)a_1(a_2 + b_c P_1^*)}. \quad (16)$$

Finally, substituting Equation (16) back into the condition $\det(M(k_c)) = 0$ (noting that $|k_c|^{\phi+\psi} = |k_c|^\phi \cdot |k_c|^\psi$) leads to the transcendental equation for the critical cross-diffusion threshold b_c :

$$-\frac{\phi}{\phi + \psi} H(b_c) \left[\frac{\psi H(b_c)}{(\phi + \psi)a_1(a_2 + b_c P_1^*)} \right]^{\psi/\phi} = \mathcal{J}_{12}\mathcal{J}_{21}. \quad (17)$$

The exponent ψ/ϕ in Equation (17) is the key mathematical factor explaining why b_c shifts significantly when $\phi \neq \psi$. If $\phi = \psi$, the above equation reduces to $\frac{1}{2}H(b_c) \left[\frac{H(b_c)}{2a_1(a_2 + b_c P_1^*)} \right] = \mathcal{J}_{12}\mathcal{J}_{21}$, which is exactly $H(b_c)^2 = 4a_1(a_2 + b_c P_1^*)\mathcal{J}_{12}\mathcal{J}_{21}$. If $\psi < \phi$ (long-range zooplankton movement), the required cross-diffusion b_c to trigger Turing instability is generally lower, explaining the accelerated pattern formation.

This is fundamentally different from the integer-order case where b_c is independent of the diffusion structure. Moreover, the fractional orders ϕ and ψ directly modulate the critical threshold for pattern formation: (a) As $\phi \rightarrow 2^-$ and $\psi \rightarrow 2^-$, k_c recovers the classical result; (b) for $\phi < 2$ or $\psi < 2$, the factor $\frac{\psi}{\phi+\psi}$ modifies the critical wavelength; (c) the growth rate at criticality: $\text{Re}(\lambda(k_c)) \propto (b - b_c)$ with modified time scale.

To quantify the impact of the fractional orders ϕ , ψ and the cross-diffusion coefficient b on the system's stability, we numerically evaluate the dispersion relation derived in Equation (12b). As illustrated in Figure 1, the introduction of anomalous diffusion fundamentally alters the Turing bifurcation behavior compared to the classical case.

Specifically, while the integer-order system ($\phi = 2.0, \psi = 2.0$) requires a critical cross-diffusion threshold of $b_c = 0.1248$ to trigger instability, fractional-order kinetics can induce instability at significantly lower thresholds. For instance, at a sub-critical value of $b = 0.12$ (Figure 1a), where the integer-order system remains stable, parameter combinations with lower ψ (e.g., $\psi = 1.8$) already exhibit positive maximum eigenvalues. This result confirms that super-diffusive zooplankton movement expands the Turing instability domain, effectively destabilizing the homogeneous steady state in regimes that would otherwise be stable.

Furthermore, once the system enters the instability regime (e.g., $b = 0.155$, Figure 1b), the fractional orders dictate the spatial scale of the emerging patterns. Higher fractional orders (closer to 2.0) are associated with smaller critical wavenumbers k_c (longer wavelengths) and faster growth rates. Conversely, lower fractional orders shift the peak eigenvalue to larger wavenumbers (shorter wavelengths) with reduced growth rates. This analysis indicates that ϕ and ψ act not only as diffusion coefficients but as selection mechanisms that control both the formation speed and the characteristic size of the spatial patterns.

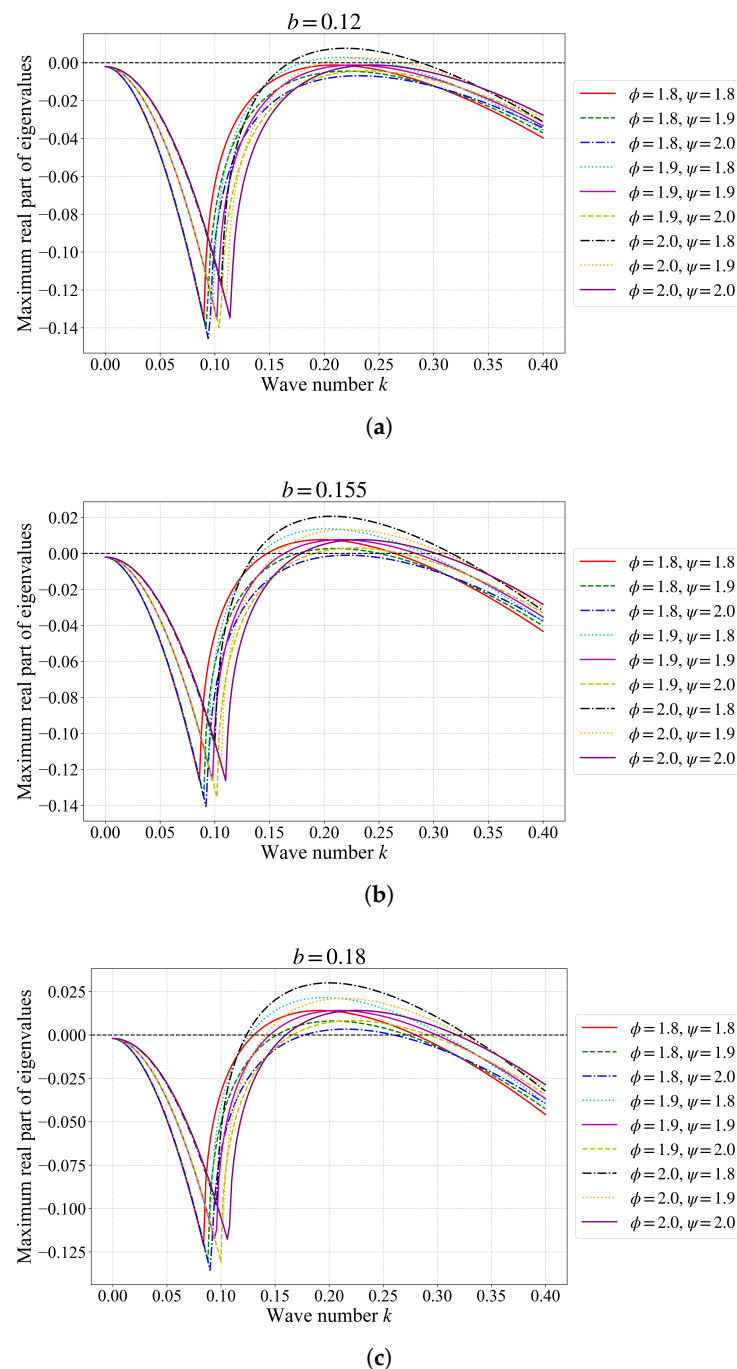


Figure 1. Maximum values of real part of eigenvalues with the variations of wave number k . Parameters: $r = 0.6$, $\alpha = 0.7$, $\beta = 0.5$, $\theta = 0.48$, $d = 0.012$, $c = 4.18$, $e = 0.05$, $a_1 = 20.0$, $a_2 = 0.1$, $K = 8$, $m = -5$.

2.3. Amplitude Equations and Pattern Selection

While the linear stability analysis described above effectively identifies the critical threshold (b_c) and the critical wavenumber (k_c) for the onset of instability, it is insufficient to fully characterize the pattern formation process. Linear theory predicts the exponential growth of perturbations but fails to account for the saturation effects induced by nonlinear interactions as amplitudes increase. Consequently, linear analysis cannot determine which specific pattern morphology (e.g., stripes, hexagons, or mixed states) will be selected, nor can it assess the stability of these emerging structures. To address this limitation and rigorously investigate the pattern selection mechanism near the bifurcation point ($b \approx b_c$), we proceed with a weakly nonlinear analysis. By employing the method of multiple scales,

we derive the Stuart–Landau amplitude equations, which govern the slow evolution of the dominant modes and allow us to determine the stability of various Turing patterns. First, We rewrite the system (2) at the positive coexistence equilibria $E_1^*(P_1^*, Z_1^*)$ as follows, denoting $\mathbf{u} = (p, z)^T$ as perturbations $(P - P_1^*, Z - Z_1^*)^T$:

$$\partial_t \mathbf{u} = \mathcal{L} \mathbf{u} + \mathbf{N} \quad (18)$$

where the linear operator $\mathcal{L}$ is defined as:

$$\mathcal{L} := \begin{pmatrix} \mathcal{J}_{11} & \mathcal{J}_{12} \\ \mathcal{J}_{21} & 0 \end{pmatrix} - \begin{pmatrix} a_1(-\Delta)^{\psi/2} & 0 \\ bZ_1^*(-\Delta)^{\psi/2} & (a_1 + bP_1^*)(-\Delta)^{\psi/2} \end{pmatrix} \quad (19)$$

and $\mathbf{N}$ represent nonlinear terms, respectively as follows:

$$\mathbf{N} = -b(-\Delta)^{\psi/2}(0, pz)^T + \begin{pmatrix} f_{pp}p^2 + f_{pz}pz + f_{ppz}p^2z + f_{ppp}p^3 + o(\epsilon^3) \\ g_{pp}p^2 + g_{pz}pz + g_{ppz}p^2z + g_{ppp}p^3 + o(\epsilon^3) \end{pmatrix} \quad (20)$$

with

$$\begin{aligned} f_{pp} &= \frac{r[(K + m - 3P_1^*)\mathcal{R}_0^2P_1^* - (e^2P_1^{*2} - 3ce)(K - P_1^*)(P_1^* - m)]}{K\mathcal{R}_0^2P_1^*}, & f_{pz} &= \frac{\alpha(eP_1^{*2} - c)}{\mathcal{R}_0^2P_1^{*2}} \\ f_{ppz} &= \frac{\alpha e(3c - eP_1^{*2})}{\mathcal{R}_0^3P_1^{*2}}, & f_{ppp} &= \frac{r[-\mathcal{R}_0^3P_1^{*3} + e(e^2P_1^{*4} - 6ceP_1^{*2} + c^2)(K - P_1^*)(P_1^* - m)]}{K\mathcal{R}_0^3P_1^{*3}} \\ g_{pp} &= \frac{r(\beta - \theta)(e^2P_1^{*2} - 3ce)(P_1^* - m)(K - P_1^*)}{\alpha K\mathcal{R}_0^2P_1^*}, & g_{pz} &= \frac{(\beta - \theta)(c - eP_1^{*2})}{\mathcal{R}_0^2P_1^{*2}}, \\ g_{ppz} &= \frac{(\beta - \theta)(e^2P_1^{*2} - 3ce)}{\mathcal{R}_0^3P_1^{*2}}, & g_{ppp} &= \frac{r(\beta - \theta)(-e^3P_1^{*4} + 6ce^2P_1^{*2} - c^2e)(K - P_1^*)(P_1^* - m)}{\alpha K\mathcal{R}_0^3P_1^{*3}}. \end{aligned}$$

At the same time, we rewrite $\mathcal{L}$ to separate out the critical mode contribution as follows:

$$\mathcal{L} = \mathcal{L}_0 + (b - b_c)\mathcal{L}_1 \quad (21)$$

where $\mathcal{L}_0$ and $\mathcal{L}_1$ are defined as:

$$\mathcal{L}_0 := \begin{pmatrix} \mathcal{J}_{11} - a_1(-\Delta)^{\psi/2} & \mathcal{J}_{12} \\ \mathcal{J}_{21} - b_cZ_1^*(-\Delta)^{\psi/2} & -(a_2 + b_cP_1^*)(-\Delta)^{\psi/2} \end{pmatrix}, \quad (22)$$

$$\mathcal{L}_1 := \begin{pmatrix} 0 & 0 \\ -Z_1^*(-\Delta)^{\psi/2} & -P_1^*(-\Delta)^{\psi/2} \end{pmatrix} \quad (23)$$

To derive the amplitude equations, we employ the method of multiple scales to obtain a solution that is uniformly valid in time. We postulate an expansion of the form:

$$\mathbf{u} = \epsilon(p_1, z_1)^T + \epsilon^2(p_2, z_2)^T + \epsilon^3(p_3, z_3)^T + o(\epsilon^3) \quad (24)$$

We simultaneously expand the control parameter b and the nonlinear terms $\mathbf{N}$ as:

$$b = b_c + \epsilon b_1 + \epsilon^2 b_2 + \epsilon b_3 + o(\epsilon^3), \quad \mathbf{N} = \epsilon^2 \mathbf{N}_2 + \epsilon^3 \mathbf{N}_3 + o(\epsilon^3) \quad (25)$$

where

$$\mathbf{N}_2 = \begin{pmatrix} f_{pp}p_1^2 + f_{pz}p_1z_1 \\ g_{pp}p_1^2 + g_{pz}p_1z_1 \end{pmatrix}, \quad \mathbf{N}_3 = \begin{pmatrix} 2f_{pp}p_1p_2 + f_{pz}(p_1z_2 + p_2z_1) + f_{ppz}p_1^2z_1 + f_{ppp}p_1^3 \\ 2g_{pp}p_1p_2 + g_{pz}(p_1z_2 + p_2z_1) + g_{ppz}p_1^2z_1 + g_{ppp}p_1^3 \end{pmatrix} \quad (26)$$

Then, by introducing time scales $T_1 = \epsilon t$, $T_2 = \epsilon^2 t$, $T_3 = \epsilon^3 t$, we rewrite the time derivative as:

$$\partial_t = \epsilon \partial_{T_1} + \epsilon^2 \partial_{T_2} + \epsilon^3 \partial_{T_3} + o(\epsilon^3) \quad (27)$$

Substituting these expansions into the governing equation and collecting terms at each order of ϵ , we obtain a hierarchy of equations.

At $O(\epsilon)$, we have:

$$\mathcal{L}_0(p_1, z_1)^T = 0 \quad (28)$$

The solution to this equation can be expressed as a superposition of critical modes:

$$(p_1, z_1)^T = (\Phi, 1)^T \sum_{j=1}^3 A_j e^{i\mathbf{k}_j \cdot \mathbf{r}} + c.c. \quad (29)$$

where $\Phi = -\mathcal{J}_{12}/(\mathcal{J}_{11} - a_1 k_c^\phi)$ and A_j are the complex amplitudes of the modes with wavevectors $\mathbf{k}_j$, satisfying $|\mathbf{k}_j| = k_c$, $c.c.$ denotes the complex conjugate.

At $O(\epsilon^2)$, we have:

$$\mathcal{L}_0(p_2, z_2)^T = \partial_{T_1}(p_1, z_1)^T - b_1 \mathcal{L}_1(p_1, z_1)^T + b_c(-\Delta)^{\psi/2}(0, p_1 z_1)^T - \mathbf{N}_2 \quad (30)$$

Denote the vector on the right-hand side of (30) as $(F_p, F_z)^T$. To ensure solvability, we require that $(F_p, F_z)^T$ is orthogonal to the null space of the adjoint operator $\mathcal{L}_0^*$. This condition leads to the first set of amplitude equations:

$$(1, \Psi) \cdot (F_p^j, F_z^j)^T = 0 \quad (31)$$

where $\Psi = -(\mathcal{J}_{11} - a_1 k_c^\phi)/(\mathcal{J}_{21} - b_c Z_1^* k_c^\psi)$ and $(F_p^j, F_z^j)^T$ are the components of $(F_p, F_z)^T$ corresponding to the mode with wavevector $\mathbf{k}_j$. This leads to:

$$\begin{cases} (\Phi + \Psi) \partial_{T_1} A_1 = -b_1 k_c^\psi (P_1^* + Z_1^* \Phi) \Psi A_1 + \\ \quad [2f_{pp} \Phi^2 + 2f_{pz} \Phi + \Psi(2g_{pp} \Phi^2 + 2g_{pz} \Phi - 2b_c k_c^\psi \Phi)] \bar{A}_2 \bar{A}_3, \\ (\Phi + \Psi) \partial_{T_1} A_2 = -b_1 k_c^\psi (P_1^* + Z_1^* \Phi) \Psi A_2 + \\ \quad [2f_{pp} \Phi^2 + 2f_{pz} \Phi + \Psi(2g_{pp} \Phi^2 + 2g_{pz} \Phi - 2b_c k_c^\psi \Phi)] \bar{A}_3 \bar{A}_1, \\ (\Phi + \Psi) \partial_{T_1} A_3 = -b_1 k_c^\psi (P_1^* + Z_1^* \Phi) \Psi A_3 + \\ \quad [2f_{pp} \Phi^2 + 2f_{pz} \Phi + \Psi(2g_{pp} \Phi^2 + 2g_{pz} \Phi - 2b_c k_c^\psi \Phi)] \bar{A}_1 \bar{A}_2. \end{cases} \quad (32)$$

At $O(\epsilon^2)$, the presence of quadratic nonlinear terms generates higher-order harmonic modes and mean flow components. Consequently, the solution $(p_2, z_2)^T$ takes the form

of a superposition of these interaction modes. We express the solution as the following Fourier series:

$$(p_2, z_2)^T = \sum_{j=1}^3 (p_0, z_0)^T |A_j|^2 + (\Phi, 1)^T \sum_{j=1}^3 B_j e^{i\mathbf{k}_j \cdot \mathbf{r}} + \sum_{j=1}^3 (p_{2k}, z_{2k})^T A_j^2 e^{2i\mathbf{k}_j \cdot \mathbf{r}} \\ + \sum_{j \neq l} (p_{mix}, z_{mix})^T A_j \bar{A}_l e^{i(\mathbf{k}_j - \mathbf{k}_l) \cdot \mathbf{r}} + c.c. \quad (33)$$

Substituting the expressions of $(p_1, z_1)^T$ and (33) into (30), we can solve for the coefficients $(p_0, z_0)^T$, $(p_{2k}, z_{2k})^T$, and $(p_{mix}, z_{mix})^T$ by matching coefficients of corresponding Fourier modes, where

$$(p_0, z_0)^T = \begin{pmatrix} -\frac{2g_{pp}\Phi^2 + 2g_{pz}\Phi}{\mathcal{J}_{21}} \\ \frac{\mathcal{J}_{11}(2g_{pp}\Phi^2 + 2g_{pz}\Phi) - \mathcal{J}_{21}(2f_{pp}\Phi^2 + 2f_{pz}\Phi)}{\mathcal{J}_{12}\mathcal{J}_{21}} \end{pmatrix},$$

$$(p_{2k}, z_{2k})^T = \begin{pmatrix} \frac{(f_{pp}\Phi^2 + f_{pz}\Phi)(a_2 + b_c P_1^*)(2k_c)^\psi - (-g_{pp}\Phi^2 - g_{pz}\Phi + b_c(2k_c)^\psi\Phi)\mathcal{J}_{12}}{(\mathcal{J}_{11} - a_1(2k_c)^\psi)(- (a_2 + b_c P_1^*)(2k_c)^\psi) - \mathcal{J}_{12}(\mathcal{J}_{21} - b_c Z_1^*(2k_c)^\psi)} \\ \frac{(-g_{pp}\Phi^2 - g_{pz}\Phi + b_c(2k_c)^\psi\Phi)(\mathcal{J}_{11} - a_1(2k_c)^\psi) - (-f_{pp}\Phi^2 - f_{pz}\Phi)(\mathcal{J}_{21} - b_c Z_1^*(2k_c)^\psi)}{(\mathcal{J}_{11} - a_1(2k_c)^\psi)(- (a_2 + b_c P_1^*)(2k_c)^\psi) - \mathcal{J}_{12}(\mathcal{J}_{21} - b_c Z_1^*(2k_c)^\psi)} \end{pmatrix}, \quad (34)$$

$$(p_{mix}, z_{mix})^T = \begin{pmatrix} \frac{(a_2 + b_c P_1^*)(2f_{pp}\Phi^2 + 2f_{pz}\Phi)(\sqrt{3}k_c)^\psi - \mathcal{J}_{12}(-2g_{pp}\Phi^2 - 2g_{pz}\Phi + b_c(\sqrt{3}k_c)^\psi\Phi)}{(\mathcal{J}_{11} - a_1(\sqrt{3}k_c)^\psi)(- (a_2 + b_c P_1^*)(\sqrt{3}k_c)^\psi) - \mathcal{J}_{12}(\mathcal{J}_{21} - b_c Z_1^*(\sqrt{3}k_c)^\psi)} \\ \frac{(\mathcal{J}_{11} - a_1(\sqrt{3}k_c)^\psi)(-2g_{pp}\Phi^2 - 2g_{pz}\Phi + b_c(\sqrt{3}k_c)^\psi\Phi) - (\mathcal{J}_{21} - b_c Z_1^*(\sqrt{3}k_c)^\psi)(-2f_{pp}\Phi^2 - 2f_{pz}\Phi)}{(\mathcal{J}_{11} - a_1(\sqrt{3}k_c)^\psi)(- (a_2 + b_c P_1^*)(\sqrt{3}k_c)^\psi) - \mathcal{J}_{12}(\mathcal{J}_{21} - b_c Z_1^*(\sqrt{3}k_c)^\psi)} \end{pmatrix}$$

At $O(\epsilon^3)$, we have:

$$\mathcal{L}_0(p_3, z_3)^T = \partial_{T_1}(p_2, z_2)^T + \partial_{T_2}(p_1, z_1)^T - b_1 \mathcal{L}_1(p_2, z_2)^T - b_2 \mathcal{L}_1(p_1, z_1)^T \\ + b_c(-\Delta)^{\psi/2}(0, p_1 z_2 + p_2 z_1)^T + b_1(-\Delta)^{\psi/2}(0, p_1 z_1)^T - \mathbf{N}_3 \quad (35)$$

Substituting the expressions of the first-order approximation $(p_1, z_1)^T$ and the second-order approximation $(p_2, z_2)^T$ into the above equation, we denote the right-hand side as $(G_p, G_z)^T$. To apply the Fredholm solvability condition, we need to isolate the resonant components that lead to secular terms. Let $(G_p^1, G_z^1)^T$ denote the coefficient vector corresponding to the critical mode $e^{i\mathbf{k}_1 \cdot \mathbf{r}}$ in the inhomogeneous term. Through detailed algebraic manipulation, we obtain:

$$G_p^1 = \Phi \partial_{T_1} B_1 + \Phi \partial_{T_2} A_1 - (2\Phi f_{pp} + f_{pz})[p_0 A_1(|A_1|^2 + |A_2|^2 + |A_3|^2) + \Phi(\bar{A}_2 \bar{B}_3 + \bar{A}_3 \bar{B}_2) \\ + p_{mix} A_1(|A_2|^2 + |A_3|^2) + p_{2k} A_1 |A_1|^2] - \Phi f_{pz}[z_0 A_1(|A_1|^2 + |A_2|^2 + |A_3|^2) + \bar{A}_2 \bar{B}_3 \\ + \bar{A}_3 \bar{B}_2 + z_{mix} A_1(|A_2|^2 + |A_3|^2) + z_{2k} A_1 |A_1|^2] - 3f_{ppz}\Phi^2 A_1(|A_1|^2 + 2|A_2|^2 + 2|A_3|^2) \\ - 3f_{ppp}\Phi^3 A_1(|A_1|^2 + 2|A_2|^2 + 2|A_3|^2) \\ = \Phi \partial_{T_1} B_1 + \Phi \partial_{T_2} A_1 + (\xi_1 |A_1|^2 + \xi_2(|A_2|^2 + |A_3|^2))A_1 - (2\Phi^2 f_{pp} + 2\Phi f_{pz})(\bar{A}_2 \bar{B}_3 + \bar{A}_3 \bar{B}_2),$$

$$\begin{aligned}
G_z^1 = & \partial_{T_1} B_1 + \partial_{T_2} A_1 + b_1 k_c^\psi (\Phi Z_1^* + P_1^*) B_1 + b_2 k_c^\psi (\Phi Z_1^* + P_1^*) A_1 + 2b_1 k_c^\psi \Phi \bar{A}_2 \bar{A}_3 \\
& - (2\Phi g_{pp} + g_{pz} - b_c k_c^\psi) [p_0 A_1 (|A_1|^2 + |A_2|^2 + |A_3|^2) + \Phi (\bar{A}_2 \bar{B}_3 + \bar{A}_3 \bar{B}_2) \\
& + p_{mix} A_1 (|A_2|^2 + |A_3|^2) + p_{2k} A_1 |A_1|^2] - (\Phi g_{pz} - b_c k_c^\psi \Phi) [z_0 A_1 (|A_1|^2 + |A_2|^2 + |A_3|^2) \\
& + \bar{A}_2 \bar{B}_3 + \bar{A}_3 \bar{B}_2 + z_{mix} A_1 (|A_2|^2 + |A_3|^2) + z_{2k} A_1 |A_1|^2] \\
& - 3g_{ppz} \Phi^2 A_1 (|A_1|^2 + 2|A_2|^2 + 2|A_3|^2) - 3g_{ppp} \Phi^3 A_1 (|A_1|^2 + 2|A_2|^2 + 2|A_3|^2) \\
= & \partial_{T_1} B_1 + \partial_{T_2} A_1 + k_c^\psi (\Phi Z_1^* + P_1^*) (b_1 B_1 + b_2 A_1) + 2b_1 k_c^\psi \Phi \bar{A}_2 \bar{A}_3 \\
& + (\eta_1 |A_1|^2 + \eta_2 (|A_2|^2 + |A_3|^2)) A_1 - (2\Phi^2 g_{pp} + 2\Phi g_{pz} - 2b_c k_c^\psi \Phi) (\bar{A}_2 \bar{B}_3 + \bar{A}_3 \bar{B}_2),
\end{aligned}$$

where

$$\begin{aligned}
\zeta_1 = & -(p_{2k} + p_0)(2\Phi f_{pp} + f_{pz}) - \Phi f_{pz}(z_{2k} + z_0) - 3f_{ppp} \Phi^3 - 3f_{ppz} \Phi^2 \\
\zeta_2 = & -(p_{mix} + p_0)(2\Phi f_{pp} + f_{pz}) - \Phi f_{pz}(z_{mix} + z_0) - 6f_{ppp} \Phi^3 - 6f_{ppz} \Phi^2, \\
\eta_1 = & -(p_{2k} + p_0)(2\Phi g_{pp} + g_{pz} - b_c k_c^\psi) - (\Phi g_{pz} - b_c k_c^\psi \Phi)(z_{2k} + z_0) - 3g_{ppp} \Phi^3 - 3g_{ppz} \Phi^2, \\
\eta_2 = & -(p_{mix} + p_0)(2\Phi g_{pp} + g_{pz} - b_c k_c^\psi) - (\Phi g_{pz} - b_c k_c^\psi \Phi)(z_{mix} + z_0) - 6g_{ppp} \Phi^3 - 6g_{ppz} \Phi^2,
\end{aligned}$$

Due to the rotational symmetry of the system, the resonant terms for the other two modes, $(G_p^2, G_z^2)^T$ and $(G_p^3, G_z^3)^T$, can be obtained by cyclic permutation of the indices. To ensure the existence of uniform bounded solutions for the third-order approximation, the Fredholm solvability condition requires that the inhomogeneous vector field be orthogonal to the kernel of the adjoint operator $\mathcal{L}_0^*$. Specifically, we impose the orthogonality condition $(1, \Psi) \cdot (G_p^j, G_z^j)^T = 0$ for $j = 1, 2, 3$. This leads to the final set of amplitude equations:

$$\left\{ \begin{aligned}
(\Phi + \Psi)(\partial_{T_1} B_1 + \partial_{T_2} A_1) = & -k_c^\psi \Psi (\Phi Z_1^* + P_1^*) (b_1 B_1 + b_2 A_1) - 2b_1 k_c^\psi \Phi \Psi \bar{A}_2 \bar{A}_3 \\
& + [2\Phi^2 f_{pp} + 2\Phi f_{pz} + \Psi(2\Phi^2 g_{pp} + 2\Phi g_{pz} - 2b_c k_c^\psi \Phi)] \\
& \times (\bar{A}_2 \bar{B}_3 + \bar{A}_3 \bar{B}_2) \\
& - [(\zeta_1 + \Psi \eta_1) |A_1|^2 + (\zeta_2 + \Psi \eta_2) (|A_2|^2 + |A_3|^2)] A_1, \\
(\Phi + \Psi)(\partial_{T_1} B_2 + \partial_{T_2} A_2) = & -k_c^\psi \Psi (\Phi Z_1^* + P_1^*) (b_1 B_2 + b_2 A_2) - 2b_1 k_c^\psi \Phi \Psi \bar{A}_3 \bar{A}_1 \\
& + [2\Phi^2 f_{pp} + 2\Phi f_{pz} + \Psi(2\Phi^2 g_{pp} + 2\Phi g_{pz} - 2b_c k_c^\psi \Phi)] \\
& \times (\bar{A}_3 \bar{B}_1 + \bar{A}_1 \bar{B}_3) \\
& - [(\zeta_1 + \Psi \eta_1) |A_2|^2 + (\zeta_2 + \Psi \eta_2) (|A_3|^2 + |A_1|^2)] A_2, \\
(\Phi + \Psi)(\partial_{T_1} B_3 + \partial_{T_2} A_3) = & -k_c^\psi \Psi (\Phi Z_1^* + P_1^*) (b_1 B_3 + b_2 A_3) - 2b_1 k_c^\psi \Phi \Psi \bar{A}_1 \bar{A}_2 \\
& + [2\Phi^2 f_{pp} + 2\Phi f_{pz} + \Psi(2\Phi^2 g_{pp} + 2\Phi g_{pz} - 2b_c k_c^\psi \Phi)] \\
& \times (\bar{A}_1 \bar{B}_2 + \bar{A}_2 \bar{B}_1) \\
& - [(\zeta_1 + \Psi \eta_1) |A_3|^2 + (\zeta_2 + \Psi \eta_2) (|A_1|^2 + |A_2|^2)] A_3,
\end{aligned} \right. \quad (36)$$

By combining the perturbation expansion $\mathcal{A}_j = \epsilon A_j + \epsilon^2 B_j + O(\epsilon^3)$ with the time derivative relation in (27), we reconstruct the unified Stuart–Landau amplitude equations corresponding to the amplitudes $\mathcal{A}_j$ ($j = 1, 2, 3$) as follows:

$$\left\{ \begin{aligned}
\tau_0 \partial_t \mathcal{A}_1 = & \mu \mathcal{A}_1 + \nu \bar{\mathcal{A}}_2 \bar{\mathcal{A}}_3 - [g_1 |\mathcal{A}_1|^2 + g_2 (|\mathcal{A}_2|^2 + |\mathcal{A}_3|^2)] \mathcal{A}_1, \\
\tau_0 \partial_t \mathcal{A}_2 = & \mu \mathcal{A}_2 + \nu \bar{\mathcal{A}}_1 \bar{\mathcal{A}}_3 - [g_1 |\mathcal{A}_2|^2 + g_2 (|\mathcal{A}_1|^2 + |\mathcal{A}_3|^2)] \mathcal{A}_2, \\
\tau_0 \partial_t \mathcal{A}_3 = & \mu \mathcal{A}_3 + \nu \bar{\mathcal{A}}_1 \bar{\mathcal{A}}_2 - [g_1 |\mathcal{A}_3|^2 + g_2 (|\mathcal{A}_1|^2 + |\mathcal{A}_2|^2)] \mathcal{A}_3,
\end{aligned} \right. \quad (37)$$

where the coefficients are defined as:

$$\begin{aligned}\tau_0 &= -\frac{\Phi + \Psi}{b_c k_c^\psi (P_1^* + \Phi Z_1^*) \Psi}, \quad \mu = \frac{b - b_c}{b_c}, \quad g_1 = -\frac{\xi_1 + \Psi \eta_1}{b_c k_c^\psi (P_1^* + \Phi Z_1^*) \Psi}, \quad g_2 = -\frac{\xi_2 + \Psi \eta_2}{b_c k_c^\psi (P_1^* + \Phi Z_1^*) \Psi}, \\ \nu &= \frac{2(b - b_c)\Phi}{b_c (P_1^* + \Phi Z_1^*)} - \frac{2f_{pp}\Phi^2 + 2f_{pz}\Phi + \Psi(2g_{pp}\Phi^2 + 2g_{pz}\Phi - 2b_c k_c^\psi \Phi)}{b_c k_c^\psi (P_1^* + \Phi Z_1^*) \Psi}.\end{aligned}\quad (38)$$

Introducing the polar coordinate transformation $\mathcal{A}_j = R_j \exp(i\vartheta_j)$ into Equation (37), we obtain the coupled system for the mode amplitudes R_j and the total phase $\Theta = \vartheta_1 + \vartheta_2 + \vartheta_3$:

$$\begin{cases} \tau_0 \partial_t \Theta = -\nu \frac{R_1^2 R_2^2 + R_1^2 R_3^2 + R_2^2 R_3^2}{R_1 R_2 R_3} \sin \Theta, \\ \tau_0 \partial_t R_1 = \mu R_1 + \nu R_2 R_3 \cos \Theta - g_1 R_1^3 - g_2 (R_2^2 + R_3^2) R_1, \\ \tau_0 \partial_t R_2 = \mu R_2 + \nu R_1 R_3 \cos \Theta - g_1 R_2^3 - g_2 (R_1^2 + R_3^2) R_2, \\ \tau_0 \partial_t R_3 = \mu R_3 + \nu R_1 R_2 \cos \Theta - g_1 R_3^3 - g_2 (R_1^2 + R_2^2) R_3. \end{cases} \quad (39)$$

Following the standard weakly nonlinear analysis near the onset of instability ($b \approx b_c$), the spatial patterns can be rigorously described as the superposition of three pairs of Fourier modes $(\mathbf{k}_j, -\mathbf{k}_j)_{j=1,2,3}$ making angles of $2\pi/3$ on the critical circle $|\mathbf{k}| = k_c$. Based on the stability theorem for the cubic amplitude equations (Theorem 4.1 in [28]), the classification and stability of the stationary solutions are summarized as follows:

Stripe Patterns (S): The stripe solution is characterized by a single pair of modes (e.g., $|\mathcal{A}_1| \neq 0, \mathcal{A}_2 = \mathcal{A}_3 = 0$), given by $R_1 = \sqrt{\mu/g_1}$. In the Fourier spectrum, this corresponds to two symmetric peaks at $\pm \mathbf{k}_1$.

- Theoretically, stripes are stable only when the cross-saturation coefficient dominates the self-saturation coefficient (i.e., $g_2 > g_1$) and the control parameter satisfies $\mu > \mu_3$.
- Otherwise, if $g_1 > g_2$, the stripe pattern is always unstable regardless of μ .

Hexagon Patterns (H_0 or H_π): Hexagons arise from the resonance of three wave vectors satisfying $\mathbf{k}_1 + \mathbf{k}_2 + \mathbf{k}_3 = 0$. The solution satisfies $R_1 = R_2 = R_3 = R^\pm$. The power spectrum exhibits six symmetric peaks forming a regular hexagon.

- These patterns exist for $\mu > \mu_1$. The solution branch R^+ is stable in the range $\mu < \mu_4$.
- The condition $\mu < \mu_4$ implies that hexagonal spots are typically the first structures to emerge from the homogeneous state (subcritical bifurcation) due to the quadratic nonlinearity ν .

Mixed States: In this study, mixed states are defined as the spatial coexistence of stripe and hexagonal patterns within the computational domain. These states typically emerge in the bistability region ($\mu_3 < \mu < \mu_4$), where both morphologies correspond to stable attractors. Consequently, the system exhibits a spatially heterogeneous structure, characterized by local patches of stripes and hexagons separated by interfaces or grain boundaries, rather than a global single-mode pattern.

The critical bifurcation thresholds μ_i derived from the coefficients g_1, g_2, ν are defined as:

$$\mu_1 = \frac{-\nu^2}{4(g_1 + 2g_2)}, \quad \mu_3 = \frac{\nu^2 g_1}{(g_2 - g_1)^2}, \quad \mu_4 = \frac{\nu^2 (2g_1 + g_2)}{(g_2 - g_1)^2}. \quad (40)$$

To visually determine the selection of patterns, we plot the control parameter μ and the stability boundaries μ_1, μ_3, μ_4 as functions of the cross-diffusion coefficient b . Figure 2 illustrates the stability diagram for the fractional orders $\phi = 1.9$ and $\psi = 1.9$.

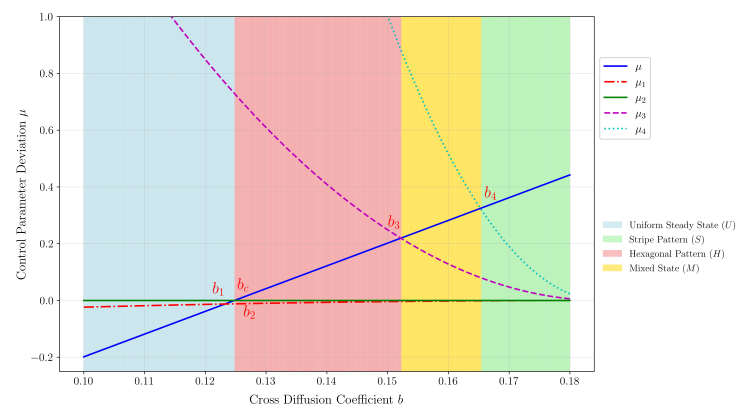


Figure 2. Stability diagram of stationary patterns as a function of the cross-diffusion coefficient b with fractional orders $\phi = 1.9$ and $\psi = 1.9$. The blue solid line represents the dependence of the control parameter μ on b . The dashed and dotted lines represent the critical stability boundaries μ_1, μ_3 , and μ_4 . The intersections of μ with these boundaries determine the critical thresholds b_c, b_3 , and b_4 , which partition the parameter space into four distinct regimes: the Uniform Steady State (U , blue region) for $b < b_c$; the Hexagonal Pattern (H , pink region) for $b_c < b < b_3$; the Mixed State (M , yellow region) for $b_3 < b < b_4$; and the Stripe Pattern (S , green region) for $b > b_4$.

As shown in Figure 2, the intersections of the curve $\mu(b)$ with the critical boundaries define specific transition points for pattern selection:

- b_c corresponds to the Turing bifurcation threshold where $\mu = 0$. For $b < b_c$, the uniform steady state is stable.
- b_3 is the threshold where $\mu = \mu_3$. The region $b_c < b < b_3$ corresponds to $\mu < \mu_3$, where the stripe mode is unstable, leading to the emergence of mixed or spot-like states.
- b_4 is the threshold where $\mu = \mu_4$. The region $b_3 < b < b_4$ satisfies $\mu_3 < \mu < \mu_4$, which is the bistability region where hexagonal patterns are stable (and stripes are also theoretically stable).
- For $b > b_4$, we have $\mu > \mu_4$, where the hexagonal mode becomes unstable, leaving the stripe pattern as the sole stable attractor.

This diagram provides a graphical map for predicting the dominant morphology based on the cross-diffusion intensity b .

3. Numerical Simulations

3.1. Numerical Methodology

To solve the fractional-order system (2), we employ a finite difference scheme combined with the Discrete Cosine Transform (DCT-II) for efficient computation of the Riesz fractional Laplacian under Neumann boundary conditions [14,29,30]. Ecologically, these zero-flux boundary conditions correspond to a closed or isolated aquatic environment (e.g., a lake or a controlled experimental mesocosm), implying that there is no net migration of phytoplankton or zooplankton across the physical boundaries of the domain. We use a uniform grid with $N \times N$ points and spatial step size dx , and an explicit Euler method with time step dt , chosen to ensure numerical stability. The Riesz fractional Laplacian $(-\Delta)^{\gamma/2}u$ is computed as follows: (a) Compute the DCT-II of u : $\hat{u} = \text{DCT-II}(u)$. (b) Multiply by the fractional eigenvalues: $\hat{u}' = \hat{u} \cdot |k|^\gamma$, where $|k|$ are the wavevectors. (c) Compute the inverse DCT-II: $u' = \text{IDCT-II}(\hat{u}')$ and apply the negative sign if needed.

We use an explicit Euler method with time step $\Delta t = 0.01$. To ensure numerical stability, the time step Δt and spatial step size dx must satisfy the fractional Courant–Friedrichs–Lewy (CFL) condition associated with the spectral derivative [31]:

$$\Delta t \leq \min\left(\frac{C(dx)^\phi}{a_1}, \frac{C(dx)^\psi}{a_2 + bP_{\max}}\right), \quad (41)$$

where C is a constant determined by the specific stability region of the time-stepping scheme and the maximum eigenvalue of the discrete fractional operator. In our simulations, the chosen Δt consistently satisfies this constraint for the range of fractional orders $\phi, \psi \in (1, 2]$ considered.

All simulations start from small random perturbations around the positive equilibrium E_1^* :

$$\begin{aligned} P(x, y, 0) &= P_1^* + \epsilon_P \cdot \mathcal{N}(0, 1), \\ Z(x, y, 0) &= Z_1^* + \epsilon_Z \cdot \mathcal{N}(0, 1), \end{aligned} \quad (42)$$

where $\mathcal{N}(0, 1)$ denotes a standard normal random variable and $\epsilon_P = 0.1P_1^*$, $\epsilon_Z = 0.1Z_1^*$.

Unless otherwise stated, we use $r = 0.6$, $\alpha = 0.7$, $\beta = 0.5$, $\Theta = 0.48$, $d = 0.012$, $c = 4.18$, $e = 0.05$, $a_1 = 20.0$, $a_2 = 0.1$, $K = 8$, $m = -5$.

3.2. Simulation Results and Analysis

3.2.1. Case 1: Fractional-Order Pattern Formation Below Classical Turing Threshold

In this case, we investigated pattern formation with parameters $b = 0.12$, $\phi = 2.0$, and $\psi = 1.8$. This parameter combination is theoretically significant because in integer-order systems, $b = 0.12$ lies below the Turing bifurcation threshold b_c , implying that no pattern formation should occur. However, our fractional-order simulations reveal a fundamentally different scenario, demonstrating the profound nonlinear effect of fractional diffusion on pattern formation.

Quantitative analysis validates this observation. Based on the derivation in Section 2.2, the critical cross-diffusion threshold for the fractional system is calculated as $b_c \approx 0.0988$ with a critical wavenumber $k_c = 0.230$. Since the chosen parameter $b = 0.12$ satisfies $b > b_c$, the system is clearly driven into the Turing instability regime. This stands in sharp contrast to the integer-order model, where the critical threshold is typically higher (e.g., $b_c \approx 0.1248$), rendering the state $b = 0.12$ stable.

Figure 3 illustrates the temporal evolution of pattern formation in the fractional-order system. At the initial time ($t = 1$), the system exhibits a nearly homogeneous state with small random fluctuations typical of initial perturbations. By $t = 500$, distinct spatial structures begin to emerge, indicating the early stages of pattern formation. This pattern emergence at sub-threshold cross-diffusion values represents a key departure from classical integer-order behavior and highlights the pattern-promoting effect of fractional diffusion. The fractional order $\psi = 1.8$ for zooplankton introduces long-range spatial correlations that effectively reduce the critical threshold b_c required for Turing instability.

By $t = 2000$, the pattern evolves into a complex mixed structure containing both hexagonal and stripe elements. To understand the selection mechanism of this morphology, we calculated the coefficients of the amplitude equations derived in Section 2.3. At $b = 0.12$, we obtained $\mu \approx 0.214$, $\nu \approx -0.053$, $g_1 \approx 0.038$, and $g_2 \approx 0.059$. The stability boundaries for different patterns were determined as $\mu_1 \approx -0.004$, $\mu_3 \approx 0.257$, and $\mu_4 \approx 1.045$. According to the standard stability theory, stripe patterns are stable only when $\mu > \mu_3$. In our simulation, the control parameter $\mu = 0.214$ falls within the range (μ_1, μ_3) , where pure stripes are unstable, but hexagonal patterns are theoretically stable (since $\mu < \mu_4$). The observation of a mixed state in the numerical simulation (Figure 3d), rather than a

pure hexagonal lattice, suggests that the system is operating in a strong competition regime. The value of μ is close enough to the stripe stability boundary μ_3 to allow stripe-like features to persist alongside hexagons, creating the complex mixed morphology. This coexistence demonstrates that the non-local effects of fractional differentiation can prolong the competition between modes, leading to diverse spatial structures unattainable in standard models.

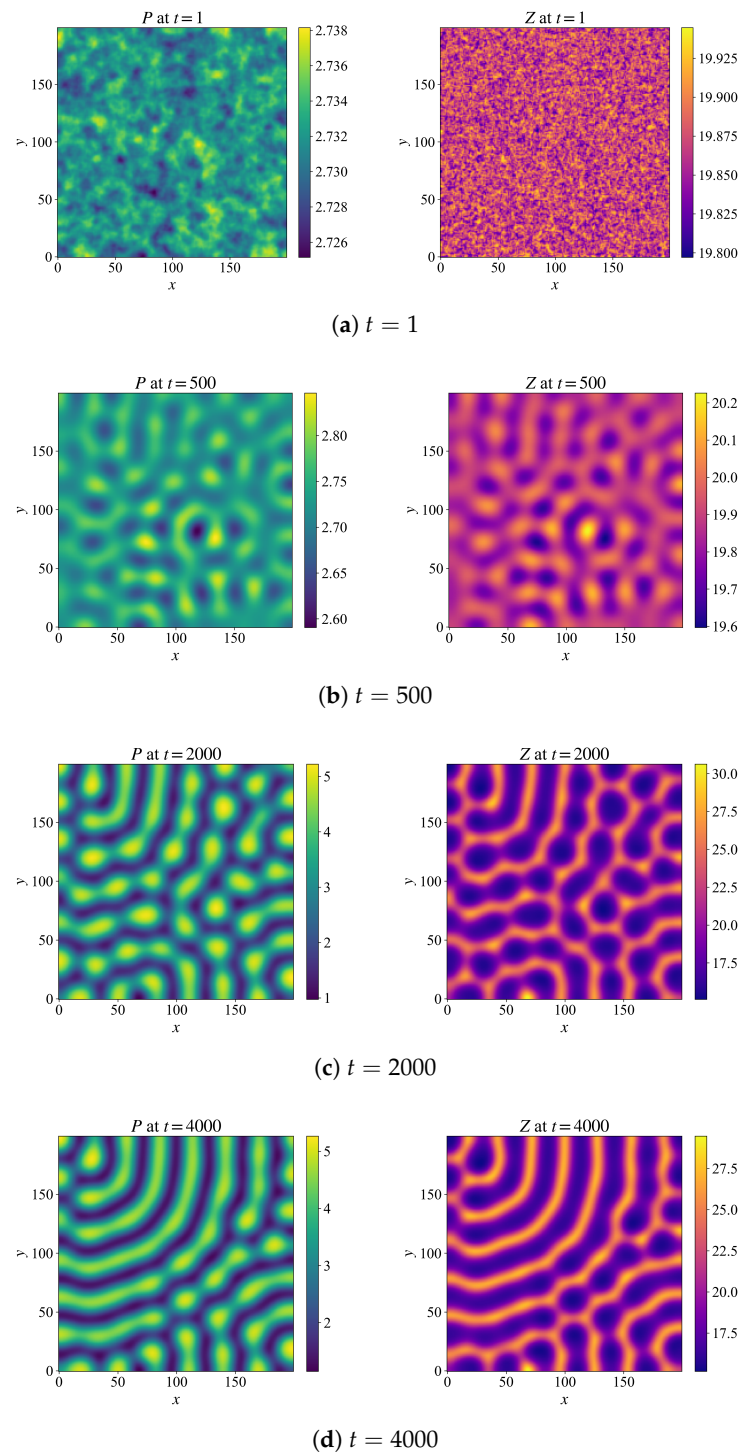


Figure 3. Pattern formation development over time. Parameters: $b = 0.12$, $\phi = 2.0$, $\psi = 1.8$.

This finding has important ecological implications: it suggests that anomalous diffusion in natural aquatic systems can lead to more diverse and complex spatial structures of plankton distributions, even under environmental conditions (represented by $b = 0.12$) that would otherwise maintain spatial homogeneity.

The physical mechanism underlying this sub-threshold pattern formation can be understood through the modified dispersion relation derived in Section 2.2. The fractional Laplacian operator $(-\Delta)^{\psi/2}$ with $\psi < 2$ introduces non-local spatial interactions that effectively amplify the destabilizing effect of cross-diffusion. This amplification shifts the Turing bifurcation curve in parameter space, allowing pattern formation at lower cross-diffusion values than in the classical case. Our numerical results confirm this theoretical prediction and demonstrate that fractional diffusion can overcome sub-threshold limitations to generate unexpected spatial complexity.

3.2.2. Case 2: Effect of Phytoplankton Fractional Order ϕ

In this case, we fixed $\psi = 2.0$ and $b = 0.18$, then systematically varied the phytoplankton fractional order ϕ from 2.0 to 1.8. This allows us to isolate how anomalous phytoplankton diffusion influences pattern selection.

Figure 4 demonstrates a distinct morphological transition in the phytoplankton density P as ϕ decreases. We utilize the amplitude equation coefficients derived in Section 2.3 to rigorously quantify the mechanism behind this transition.

At $\phi = 2.0$ (Figure 4a), corresponding to classical Gaussian diffusion, the bifurcation threshold is $b_c \approx 0.1248$. With $b = 0.18$, the control parameter $\mu \approx 0.4422$ is significantly larger than the stripe stability threshold $\mu_3 \approx 0.0051$ (and $\mu > \mu_4 \approx 0.0210$). According to the stability theory, this regime ($\mu > \mu_3$) strongly favors pure stripe patterns. Consequently, the system exhibits well-defined stripe (S) patterns, characterized by parallel bands of high and low density.

As the fractional order ϕ decreases to 1.9 (Figure 4b), the critical threshold increases to $b_c \approx 0.1408$, reducing the effective distance from criticality. The calculated parameters are $\mu \approx 0.2782$, with stability boundaries $\mu_3 \approx 0.1011$ and $\mu_4 \approx 0.4102$. Here, the system enters the bistability region defined by $\mu_3 < \mu < \mu_4$, where both stripe and hexagonal solutions are theoretically stable. This mathematical bistability manifests physically as symmetry breaking, resulting in a mixed state where elongated structures coexist with emerging spot-like elements, as the system explores the attraction basins of competing attractors.

Finally, at $\phi = 1.8$ (Figure 4c), the bifurcation threshold rises further to $b_c \approx 0.1608$, yielding a small control parameter $\mu \approx 0.1192$. Crucially, this value drops below the stripe stability threshold $\mu_3 \approx 0.3682$ (while remaining below $\mu_4 \approx 1.4789$). In this regime ($\mu > \mu_4$), the stripe and hexagonal mode become unstable. This aligns with the simulation, where the dominant morphology shifts toward localized spot or mixed (M) patterns.

This transition from stripes to spots as ϕ decreases can be understood through the modification of the dispersion relation and the diffusion kernel $a_1|k|^\phi$. As ϕ decreases, the sub-diffusive penalty on high-wavenumber modes is relatively relaxed compared to the Laplacian case ($\phi = 2$), leading to a heavy-tailed spatial coupling. This shift in the diffusion kernel favors the selection of localized spots over extended stripes, physically pushing the system back towards the onset of instability (low μ) where hexagonal patterns typically prevail. Ecologically, this suggests that more anomalous (non-local) phytoplankton movement, perhaps driven by intense turbulent mixing, tends to fragment continuous population bands into isolated patches, which may significantly impact the grazing efficiency of zooplankton and the overall stability of the aquatic ecosystem.

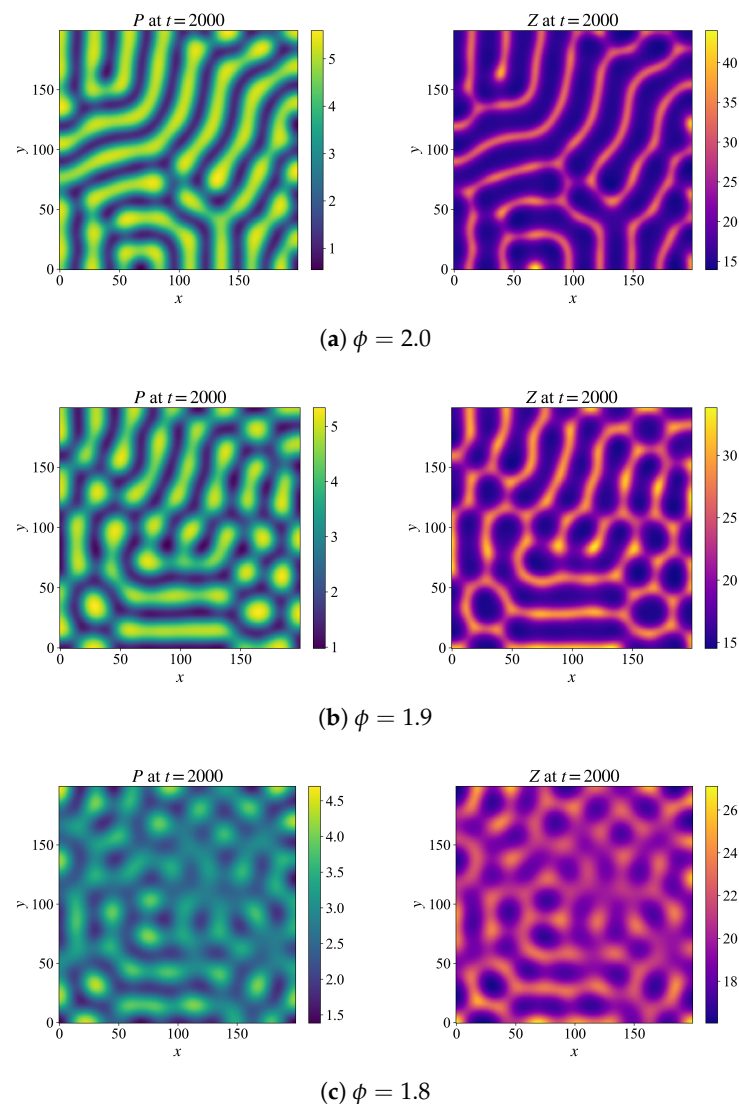


Figure 4. Pattern transition with decreasing phytoplankton fractional order ϕ . Parameters: $b = 0.18$, $\psi = 2.0$.

3.2.3. Case 3: Effect of Zooplankton Fractional Order ψ

In this case, we fixed $\phi = 1.9$ and $b = 0.155$, then varied the zooplankton fractional order ψ from 2.0 to 1.8. Figure 5 displays a distinct morphological progression that is notably opposite to the trend observed in Case 2. The quantitative bifurcation analysis provides a clear mathematical justification for this inverse morphological sequence.

At $\psi = 2.0$ (Figure 5a), where zooplankton follow classical Fickian diffusion, the critical threshold is relatively high at $b_c \approx 0.1408$. For $b = 0.155$, the control parameter is $\mu \approx 0.1006$. Analysis of the Stuart-Landau coefficients reveals that this value lies well below the stripe stability threshold ($\mu_3 \approx 0.4129$), rendering the stripe mode strictly unstable. As a result, the phytoplankton density P exhibits well-organized hexagonal (H) or spot-like patterns, corresponding to the stable region for hexagons ($\mu < \mu_4 \approx 1.6747$).

As ψ decreases to 1.9 (Figure 5b), anomalous zooplankton dispersal amplifies the cross-diffusion instability, significantly reducing the critical threshold to $b_c \approx 0.1248$. Consequently, the control parameter increases to $\mu \approx 0.2419$. With the stability boundaries calculated as $\mu_3 \approx 0.1836$ and $\mu_4 \approx 0.7399$, the system explicitly enters the bistability region defined by $\mu_3 < \mu < \mu_4$. In this regime, both hexagonal and stripe solutions are theoretically stable attractors. This strong competition between modes prevents the system

from settling into a single uniform morphology, resulting in the observed mixed state characterized by the coexistence of elongated aggregations and spot-like elements.

Finally, at $\psi = 1.8$ (Figure 5c), representing highly anomalous zooplankton movement, the threshold drops further to $b_c \approx 0.1105$, pushing the system deep into the unstable regime with $\mu \approx 0.4032$. Crucially, the stability boundaries shift to $\mu_3 \approx 0.0395$ and $\mu_4 \approx 0.1584$. Under these conditions, μ exceeds both μ_3 and μ_4 , meaning the hexagonal pattern entirely loses its stability, while the stripe pattern becomes the sole stable attractor. Thus, the morphology undergoes a complete qualitative shift toward well-defined stripe (S) patterns.

This contrasting behavior between ϕ and ψ highlights the asymmetric role of predator and prey dispersal in pattern selection. While decreasing ϕ (phytoplankton) tends to localize the population into spots by reducing the effective distance from criticality (low μ), decreasing ψ (zooplankton) facilitates the elongation and connection of these patches into stripes by pushing the system further beyond the bifurcation threshold (high μ). The physical interpretation involves the interplay between the scales of nutrient–prey interaction and predator grazing pressure: anomalous zooplankton dispersal ($\psi < 2$) allows predators to exert grazing pressure over much larger spatial scales, effectively “stretching” the prey patches into elongated stripe structures to minimize local predation risk.

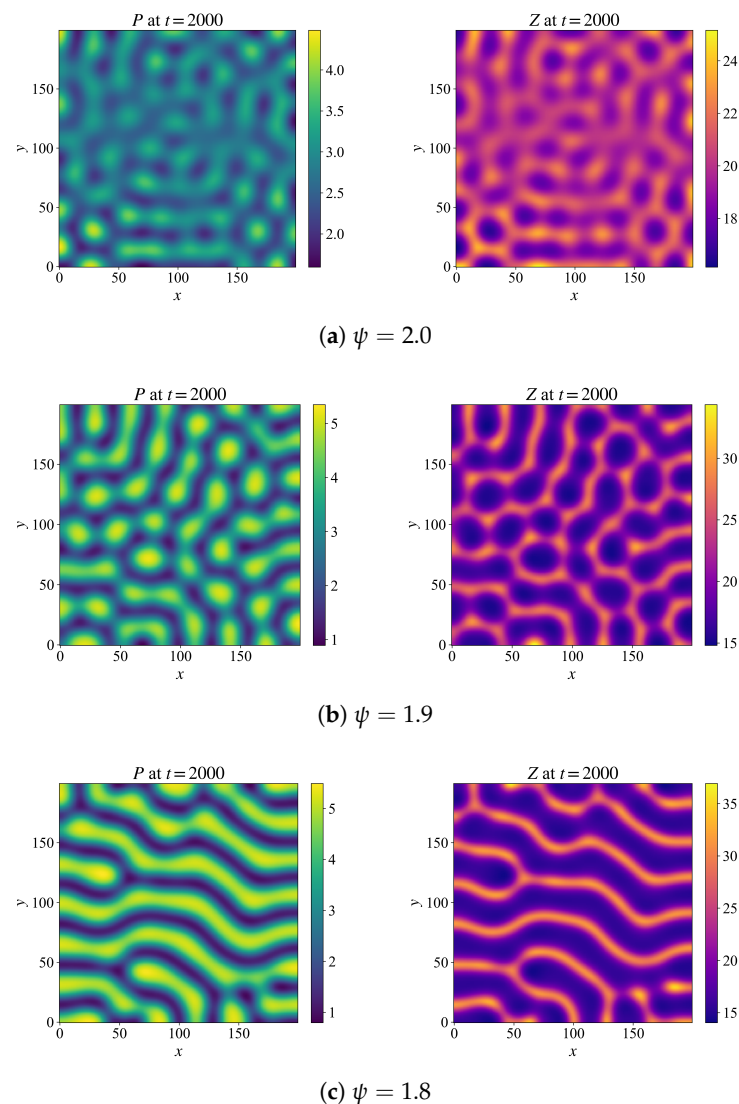


Figure 5. Pattern transition with decreasing zooplankton fractional order ψ . Parameters: $b = 0.155$, $\phi = 1.9$.

4. Discussion and Conclusions

In this study, we have investigated the effects of Riesz fractional diffusion on pattern formation in a toxic-phytoplankton–zooplankton model, extending the classical integer-order framework to incorporate species-specific anomalous diffusion through operators $(-\Delta)^{\phi/2}$ and $(-\Delta)^{\psi/2}$, where $\phi, \psi \in (1, 2]$. Our theoretical analysis rigorously derives the conditions for Turing bifurcation in the presence of fractional diffusion. A key finding is that the critical cross-diffusion threshold b_c is fundamentally modified by the exponent ratio ψ/ϕ , which distinguishes fractional-order systems from their integer-order counterparts. This mathematical modification provides a theoretical explanation for our Case 1 observation: patterns can emerge at $b = 0.12$, a value below the classical Turing bifurcation threshold, when zooplankton exhibit fractional-order dispersal ($\psi = 1.8$).

Through numerical simulations using a fractional finite difference scheme combined with the Discrete Cosine Transform (DCT-II) method, we demonstrate that fractional orders significantly affect both pattern morphology and formation dynamics. Our results reveal three primary findings: (1) species-specific fractional diffusion enables pattern formation below classical Turing thresholds, creating complex structures that are unattainable in integer-order systems; (2) the two fractional orders play distinct and opposing roles in pattern selection: decreasing the phytoplankton order ϕ promotes a transition from stripes to hexagonal spots by narrowing the unstable wavenumber range, whereas decreasing the zooplankton order ψ drives a transition from hexagons to stripes by broadening the unstable spectrum.

These findings have direct implications for understanding spatial dynamics in plankton communities. The incorporation of Riesz fractional diffusion provides a more realistic mathematical framework for modeling plankton dynamics in heterogeneous aquatic environments where classical diffusion assumptions break down due to turbulence and non-local interactions. Our species-specific approach, which separately quantifies the anomalous dispersal of passive phytoplankton and active zooplankton, represents a significant advance over models that assume identical diffusion mechanisms for all species.

Despite the insightful results regarding fractional-order pattern formation, it is important to acknowledge a limitation of the current study. Our model assumes that the fractional orders ϕ and ψ are constant parameters throughout the domain and time. However, in realistic aquatic environments, the degree of anomalous diffusion may vary spatiotemporally due to heterogeneous turbulence levels or changing environmental conditions. Modeling such complexity would require variable-order fractional operators, which presents significant theoretical and numerical challenges but remains a crucial direction for ensuring the model's ecological fidelity.

Future research will focus on: (1) incorporating both spatial and temporal fractional diffusion to investigate the interplay between anomalous transport and memory effects, specifically examining how history-dependence may induce pattern formation delays or hysteresis phenomena; and (2) comparing simulation results with high-resolution field tracking data to empirically estimate fractional orders for real-world plankton species.

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