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Patterns in natural systems

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Citation

Sewalt, L. (2016, September 8). *Patterns in natural systems*. Retrieved from <https://hdl.handle.net/1887/42756>

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Title: Patterns in natural systems

Issue Date: 2016-09-08

Stability of a benthic layer of phytoplankton¹

Abstract We consider a two-component system of evolutionary partial differential equations posed on a bounded domain. Our system is pattern forming, with a small stationary pattern bifurcating from the background state. It is also equipped with a multiscale structure, manifesting itself through the presence of spectrum close to the origin. Spatial processes are associated with long time scales and affect the nonlinear pattern dynamics strongly. To track these dynamics past the bifurcation, we develop an asymptotics-based method complementing and extending rigorous center manifold reduction. Using it, we obtain a complete analytic description of the pattern stability problem in terms of the linear stability of the background state. Through this procedure, we portray with precision how slow spatial processes can destabilize small patterns close to onset. We further illustrate our results on a model describing phytoplankton whose growth is limited by both nutrient and light. Localized colonies forming at intermediate depths are found to be subject to oscillatory destabilization shortly after emergence, whereas boundary-layer type colonies at the bottom persist. These analytic results are in excellent agreement with numerical simulations for the full model, which we also present.

The interest to model and investigate dynamic processes at the planetary level necessitates the development of analytical tools for multicomponent models. We consider a class of deterministic systems evolving both in time and space and incorporating slow, passive, spatial processes. Exploiting their multiscale structure, we develop a method to study the long-term dynamics of small spatial

¹The content of this chapter was published as *The effect of slow spatial processes on emerging spatiotemporal patterns* in *Chaos* in 2015, see [41].

patterns as they bifurcate. Our analytic results indicate that passive processes strongly affect and may even destabilize such small patterns over a long timescale. Numerical simulations for an ecologically relevant model of plankton growth in the ocean support these findings, by showing how nutrient diffusion destabilizes deep chlorophyll maxima over a timescale of several years.

As efforts to comprehend how our planet functions intensify, so does the need to comprehend the glaring spatial heterogeneity characterizing it. The trend towards investigating bona fide spatial phenomena, such as mobility or anisotropy, is plainly visible within many core Mathematics of Planet Earth areas [57, 71, 101, 103, 100, 112, 134]. That trend, however, is not always reflected in our modeling efforts. Indeed, modeling studies of natural phenomena often focus on temporal variation, without explicitly accounting for spatial variability. The resulting models can predict, elucidate or quantify temporal trends in the system under investigation, but their ability to incorporate spatial information is, unsurprisingly, limited. Despite these limitations, spatially homogeneous models enjoy wide popularity across a broad range of disciplines. Their evident ability to generate realistic, if crude, information is but one facet of that tenacity. Equally important is the confluence of their inimitable simplicity, which sets the mechanisms underlying complex phenomena in stark relief, and of a rich toolbox that enables their analysis.

Mathematically speaking, such models are typically formulated as nonlinear systems of ordinary differential equations (ODEs). As such, their analysis benefits immeasurably from the advent of dynamical systems theory, an immensely powerful conglomerate of qualitative tools dating back to Poincaré [129]. The inclusion of spatiality, on the other hand, leads to partial differential equation (PDE) models. The theoretical foundation for the qualitative analysis of nonlinear, pattern forming PDEs has been set through the work of Turing [156], but a coherent theory is still largely missing except for sufficiently close to equilibrium. This is particularly pronounced for systems of PDEs, whose global dynamics remain poorly understood and which form the subject of this short communication.

Here, we specifically focus on the dynamics of a system of two evolutionary PDEs posed in a domain of arbitrary dimension. The model is general enough to accommodate various applications, but we conceptualize it in terms of a particular setting in the interest of clarity. In particular, we consider it to track the spatial densities of a consumer and a resource, as they evolve in time and space under the influence of uptake/growth dynamics and spatial processes. We assume these spatial processes of the resource to be strictly linear and to play out much more slowly than the nonlinear dynamics associated with uptake and growth. Our expressed aim is to shed some light on the importance of spatiality, and we embark on this mission by exploring the role played by the slow, spatial

processes. We find these to be crucial, in that they strongly inform the fate of small patterns emerging from the background state. Although such patterns *emerge* when resource availability crosses a certain threshold, as in non-spatial models, their *fate* strongly depends on these processes. Depending on problem specifics, spatiality can effectively “break” what resource availability “makes”.

Our work here also serves as a blueprint for the analytic investigation of post-bifurcation dynamics relatively close to criticality but not close enough to be within reach of rigorous methods. Perhaps somewhat counter-intuitively, this analysis is not obstructed, but rather *facilitated* by the presence of long timescales associated with spatial dynamics. To appreciate this statement, note that the small pattern dynamics become nontrivial only when the unstable and longest stable timescales become commensurate. Here, these longest stable timescales correspond by design to linear spatial processes, a fact that enables us to (formally) reduce the system of two PDEs to an ODE coupled to a PDE. This formulation was also mentioned in Chapter 2, see Remark 2.1. Within that coupled system, the linear PDE dictates the evolution of the resource profile, while the nonlinear ODE dictates that of the amplitude of the emerging pattern. The *intricacy* of the resulting stability problem for that pattern is due to the infinite-dimensional character of the reduced system. Its *tractability*, on the other hand, is largely a result of our ability to generate the Green’s function for the linear PDE problem.

to include *nonlinear* spatial processes. The reduction procedure outlined above carries over to that case, yielding a fully nonlinear ODE–PDE system. Here too, the bifurcating pattern forces the evolution of the resource profile; that, in turn, feeds parametrically into the ODE for the pattern. Such nonlinearities increase in many ways the number of possible evolution scenarios, but they do so at the expense of analytic tractability. Other generalizations, such as wider classes of nonlinear terms, can also be considered. We will refrain from doing so here to keep the discussion simple.

This chapter builds on and extends prior work, most notably [176] and Chapter 2 of this thesis. In [176], we considered an explicit instantiation of the general model considered presently, namely a plankton–nutrient model posed on a water column. Our analysis there began with the derivation of ODEs for the eigenmodes and proceeded with copious amounts of asymptotics. Through that work, we tracked analytically the emerging pattern, a localized plankton population at an intermediate depth called a *deep chlorophyll maximum* (DCM), and showed that it is destabilized shortly after it bifurcates. We recapture a large part of those results much more compactly here by employing our new framework; see Section 3.3.2. In Chapter 2 of this thesis, we worked with a variety of related models. The focus there, however, was on the derivation of

finite dimensional approximations in general and on low-dimensional chaotic dynamics in particular. The part of that work concerning two-component PDE models can, in principle, be made to fit the framework developed here. In contrast to [176], little can be earned by doing that and we do not pursue that direction further. Conversely, our setting here may be easily modified to include bifurcations of higher codimension as in Chapter 2, at the moderate cost of involving *multiple* ODEs in the reduced system. We reserve this work also for a future communication, especially as it relates to the presence of a codimension 2 point in our exemplar phytoplankton-nutrient system [176].

We conclude this introductory section by outlining the work presented here. In Section 3.1, we formulate our model and a number of assumptions relating to it. Then, in Section 3.2.1, we develop an analytical method which allows us to track the emergent pattern beyond the range of validity of classical center manifold reduction. The main result here is an extension of that classical method, in the form of a coupled system composed of a nonlinear ODE and a linear PDE. Using that extension, we discuss the stability of the pattern in Section 3.2.2. In fact, we are able to express that stability problem in a surprisingly simple form, which welds particulars both of the background state and of the spatial processes. In this manner, we extend and streamline prior results from [176] and Chapter 2 where the ODE–PDE structure of the reduced problem was mentioned in 2.1 but not used extensively. Instead, we chose to work with the infinite-dimensional system of ODEs that is equivalent to it. The applicability of our methodology is illustrated in Sections 3.3–3.4, where we consider the phytoplankton–nutrient model. With the help of the theory developed in Section 3.2, we recapture the oscillatory destabilization of DCM patterns in Section 3.3.1. Relatedly, we consider another type of pattern in Section 3.4, namely boundary-layer type, benthic layer (BL) colonies at the bottom whose dynamics were previously unexamined. Such patterns require a deeper analysis that necessarily involves higher-order effects and showcases the advantages of our streamlined approach over our earlier, more direct efforts [176]. Through that analysis, we obtain a new result in itself by finding such colonies to persist in the regime we consider. Section 3.5 concludes the chapter with a summary and critical discussion of our findings.

3.1 Problem setting

We consider a class of nonlinear, slow/fast PDE systems,

$$\begin{bmatrix} u \\ v \end{bmatrix}_t = \begin{bmatrix} \mathcal{L} & 0 \\ \varepsilon \mathcal{K} & -\varepsilon \mathcal{M} \end{bmatrix} \begin{bmatrix} u \\ v \end{bmatrix} - \begin{bmatrix} f(z, u, v; \varepsilon) uv \\ \varepsilon g(z, u, v; \varepsilon) \end{bmatrix} \quad (3.1)$$

postulated for functions $u(z, t) : \Omega \times \mathbb{R}_+ \rightarrow \mathbb{R}$ and $v(z, t) : \Omega \times \mathbb{R}_+ \rightarrow \mathbb{R}$. Here, $\Omega \subset \mathbb{R}^n$ is a given bounded domain with piecewise smooth boundary, $\mathbb{R}_+$ is the positive timeline and we assume that boundary conditions guaranteeing well-posedness apply. We leave the linear differential operators $\mathcal{L}$ and $-\mathcal{M}$ unspecified but demand that their point spectra are bounded from above. Our main interest lies in reaction–diffusion systems, for which $\mathcal{L}$ and $-\mathcal{M}$ are second-order and elliptic, and we will work with such operators in the ecological application treated in Sections 3.3–3.4. Other choices are possible and have been discussed in Chapter 2. We impose no specific conditions on the linear operator $\mathcal{K}$ other than that, together with $\mathcal{M}$, it contains the linear dynamics; specifically, $g(z, u, v; \varepsilon) = \mathcal{O}(u^2 + v^2 + \varepsilon^2)$, as $(u, v, \varepsilon) \rightarrow (0, 0, 0)$. In the same vein, we demand that $f_0(z) = f(z, 0, 0; 0)$ is bounded and not identically zero, so that the leading order nonlinearity $f_0 uv$ is quadratic. More general nonlinearities, including ones with nonlocalities as in Sections 3.3–3.4, are similarly treatable. For clarity of presentation in this expository chapter, however, we refrain from considering these in detail.

The form assumed by the nonlinearity for u reflects our motivation, which is rooted in the aforementioned ecological problem. In short, u is the concentration of a *consumer* feeding on a spatially distributed *resource*. The concentration v measures resource deviation from a specific spatial profile which, in turn, is attained in the full absence of consumers. This profile represents an offset, as casting our model in terms of resource *deviation* shifts the trivial state to the origin, $(u, v) = (0, 0)$. Additionally, it is optimal for consumer growth, with growth limitations caused by depleted resources reflected in the nonlinearity g . The operator $\mathcal{L}$ models growth under optimal conditions, as well as linear spatial processes such as diffusion and advection. Similarly, $-\mathcal{M}$ models the linear spatial processes affecting the resource, with the minus sign emphasizing their stabilizing character. Here also, more general nonlinearities for u may be analyzed, but we do not pursue this direction at present.

Before proceeding with the analysis, we fix notation, which is slightly abusing compared to Chapter 2. We will write $\sigma_p(\mathcal{L}) = \{\lambda_j\}_{j \geq 0}$ and $\sigma_p(\mathcal{M}) = \{\mu_j\}_{j \geq 0}$ for the point spectra of the differential operators in system (3.1). For the former, we explicitly assume that its primary eigenvalue λ_0 is real and associated with a one-dimensional eigenspace. Further, it is separated by all other eigenvalues in $\sigma_p(\mathcal{L})$ by a spectral gap of sufficient width,

$$\varepsilon \gg \lambda_0 - \operatorname{Re}(\lambda_j) > 0, \quad \text{for all } j \geq 1. \quad (3.2)$$

For $\sigma_p(\mathcal{M})$, we demand it remains bounded away from the imaginary axis as $\varepsilon \downarrow 0$, i.e., $\operatorname{dist}(\sigma_p(\mathcal{M}), i\mathbb{R}) > M$ for some optimally chosen, positive constant M not depending on ε . Additionally, we assume $\sigma_p(\mathcal{M})$ to be bounded from below;

recall our earlier remark. We write $\{u_j\}_{j \geq 0}$ and $\{v_j\}_{j \geq 0}$ for the eigenfunctions of $\mathcal{L}$ and $\mathcal{M}$, so that $\mathcal{L}u_j = \lambda_j u_j$ and $\mathcal{M}v_j = \mu_j v_j$. Again, note that this is slightly abusive notation compared to Chapter 2. The Banach spaces spanned by $\{u_j\}_{j \geq 0}$ and $\{v_j\}_{j \geq 0}$ are denoted by $\mathbb{X}_u$ and $\mathbb{X}_v$, respectively, and (3.1) with suitable boundary conditions is well-posed on the product $\mathbb{X}_u \times \mathbb{X}_v$. We also introduce the $\mathcal{L}$ -invariant spaces $\mathbb{X}_{u,0} = \text{span}(u_0)$ and $\mathbb{X}_{u,r} = \text{cl}(\text{span}\{u_j\}_{j \geq 1})$, with the restriction of $\mathcal{L}$ on the latter satisfying $\sigma_p(\mathcal{L}|_{\mathbb{X}_{u,r}}) = \{\lambda_j\}_{j \geq 1}$; in Sections 3.3–3.4, all four spaces will be closed subspaces of $L^2(\Omega)$. Finally, we define a projection $P_0 : \mathbb{X}_u \rightarrow \mathbb{X}_{u,0}$ with $\ker(P_0) = \mathbb{X}_{u,r}$, which strips functions of their components along $u_1, u_2, \dots$. Lastly, we introduce the ‘projection amplitude’ operator $P_0^a : \mathbb{X}_u \rightarrow \mathbb{R}$ by $P_0 u = (P_0^a u) u_0$. In a Hilbert space setting, this corresponds to the inner product $P_0^a = \langle \cdot, \hat{u}_0 \rangle$, whereas $P_0 = \langle \cdot, \hat{u}_0 \rangle u_0$. Here, the function $\hat{u}_0 \in \mathbb{X}_u$ is the dual of u_0 , i.e. $\langle u_0, \hat{u}_0 \rangle = 1$ and $\langle u_0, \hat{u}_j \rangle = 0$ for all $j \geq 1$.

3.2 Emergence and evolution of a small colony

As discussed in the Introduction, understanding the emergence and interaction of spatial structures in a system helps to shed light on the appearance of complex dynamics in it. To track such patterns, we will employ a scalar parameter quantifying the ability of the environment to sustain consumers. In the model problem we treat in the next sections, this parameter measures resource abundance in the absence of consumers, i.e. it quantifies the resource offset briefly discussed in the last section. This control parameter will affect $\sigma_p(\mathcal{L})$, at the very least, so that we will effectively replace it by λ_0 in what follows: consumer populations can either grow or diminish depending on whether λ_0 is positive or negative.

Center manifold reduction captures the evolution of emerging small populations local to bifurcation – specifically, as long as λ_0 is asymptotically smaller than both $\{\lambda_j\}_{j \geq 1}$ and the bound εM on $\sigma_p(\varepsilon \mathcal{M})$. In that regime, the emerging pattern evolves on the longest timescale present in the system, and all other modes can effectively be considered equilibrated with respect to it. Here, instead, we derive reduced evolution laws that remain valid in the regime where emerging pattern and spatial processes evolve in *commensurate* timescales. In doing that, we demonstrate that the pattern dynamics are enriched substantially by interacting with the spatial component and, concurrently, we extend center manifold reduction in a natural manner.

3.2.1 An evolution law for the emerging population

Our tracking begins with the trivial state $(u, v) = (0, 0)$. Since λ_0 is real and leads all other eigenvalues in $\sigma_p(\mathcal{L})$, it can only enter the right-half complex plane through zero. At that point, the trivial equilibrium is destabilized and develops an unstable direction. For quadratic nonlinearities, such as the ones

we will consider, this is the classical setting for the transcritical bifurcation of a stable equilibrium branch $\{(u^*(z; \lambda_0), v^*(z; \lambda_0))\}$ parametrized by λ_0 . For λ_0 sufficiently small, the full model dynamics are effectively described by a single ODE for the equilibrium amplitude. That amplitude, in turn, scales with λ_0 and the dynamics about it play out on an $\mathcal{O}(1/\lambda_0)$ timescale [98].

These arguments suggest the rescaling

$$\begin{aligned} \lambda_0 &= \varepsilon \Lambda_0, & \tau &= \varepsilon t, \\ u(z, t) &= \varepsilon x(z, \tau), & v(z, t) &= \varepsilon y(z, \tau), \end{aligned}$$

for the regime $\lambda_0 = \mathcal{O}(\varepsilon)$. This is a crucial element in our approach, as classical center manifold reduction is inapplicable for $\lambda_0 = \mathcal{O}(\varepsilon)$. Indeed, in that regime, λ_0 is of the same order as the small eigenvalues $\{\varepsilon \mu_j\}_j$, with spatial processes and pattern dynamics evolving on the same timescale. To emphasize this, we decompose the u -component into eigenfunctions by means of $x(z, \tau) = x_0(\tau)u_0(z) + x_r(z, \tau)$. Here, $x_0 u_0 = P_0 x \in \mathbb{X}_{u,0}$ is the component of x in the principal eigendirection, while $x_r = (I - P_0)x \in \mathbb{X}_{u,r}$ is a remainder summarizing the components of x along all other eigendirections. Similar to center manifold reduction, the objective of this decomposition is to derive a dynamic equation for x_0 and constrain (*slave*) the remainder x_r . To that effect, we start by reporting the evolution laws for the two components,

$$\begin{aligned} \dot{x}_0 &= \Lambda_0 x_0 - P_0^a(f(z, \varepsilon x, \varepsilon y; \varepsilon)(x_0 u_0 + x_r)y), \\ \dot{x}_r &= \varepsilon^{-1} \mathcal{L}|_{\mathbb{X}_{u,r}} x_r \\ &\quad - (I - P_0)(f(z, \varepsilon x, \varepsilon y; \varepsilon)(x_0 u_0 + x_r)y). \end{aligned}$$

The regime we are interested in is $\Lambda_0 = \mathcal{O}(1)$, where the emerging pattern and the spatial processes evolve in commensurate timescales but the remainder x_r contracts much faster. Indeed, in that regime, the spectrum of $\varepsilon^{-1} \mathcal{L}|_{\mathbb{X}_{u,r}}$ is asymptotically large and resides in the left half of the complex plane, so that the remainder x_r contracts in a relatively short timescale of order $|\varepsilon/\lambda_1| \ll |1/\Lambda_0|$. This formally leads to the slaving relation (compare to [176] and those in Chapter 2)

$$\mathcal{L}|_{\mathbb{X}_{u,r}} x_r = \varepsilon x_0 (I - P_0)(f_0 u_0 y), \quad (3.3)$$

at leading order in ε , showing the remainder x_r to be higher-order. This equation supplements the *reduced* dynamic problem

$$\begin{aligned} \dot{x}_0 &= \Lambda_0 x_0 - x_0 P_0^a(f_0 u_0 y), \\ y_\tau &= -\mathcal{M}y + x_0 \mathcal{K}u_0, \end{aligned} \quad (3.4)$$

with the prescribed boundary conditions for y also applying. Note carefully that this evolutionary system is comprised of an ODE for $x_0(\tau)$ coupled to an inhomogeneous PDE for $y(z, \tau)$; that PDE is *linear*, as the nonlinearity $\varepsilon g(z, u, v; \varepsilon)$ has no leading order impact. This system is analogous to the ODE-PDE system derived for (2.2) as described in Remark 2.1. The advantage of using the ODE-PDE formulation of this reduction is mostly its compactness, although it does take away some of the grip on the amplitude equations. Since the full method is already laid out in Chapter 2, however, the current approach suits the purpose of this chapter best. In the system, the pattern drives the evolution of the profile y whereas, reversely, y forces the pattern parametrically. Note, also, that Λ_0 enters this system both explicitly, through $\Lambda_0 x_0$, and implicitly through u_0 . Typically, though, u_0 can be replaced by its $\lambda_0 = 0$ counterpart, as $\mathbb{X}_{u,0}$ will generically vary with λ_0 slower than at an $\mathcal{O}(1/\varepsilon)$ rate: $\varepsilon \|(I - P_0)du_0/d\lambda_0\| \ll \|u_0\|$. In that case, Λ_0 enters system (3.4) only explicitly.

The evolutionary system (3.4) generates a semiflow on an invariant manifold which is local to the origin and a graph over $\mathbb{X}_{u,0} \oplus \mathbb{X}_v$. By construction, that manifold also contains the bifurcating branch of equilibria and the non- (or less) transient dynamics around it. In other words, the ODE-PDE system (3.4) directly extends the one-dimensional ODE center manifold reduction further away from equilibrium and where bifurcating pattern and slow spatial processes interact at leading order. This extension is critical, as we will see below, in that it captures information about pattern evolution that center manifold reduction misses. In principle, the infinite-dimensional ODE systems derived in [176] and Chapter 2 of this thesis can be rederived directly from (3.4) by eigenmode decomposition. Conversely, (3.4) offers itself to any of various Galerkin approaches [135] but maintains a twofold advantage over them. First, it circumvents questions pertaining to the number of modes that must be retained; and second, it allows for a compact analysis by exploiting the linearity and overall simplicity of the PDE problem for y . This will become more apparent both in the next section and in the model treated in Sections 3.3–3.4.

3.2.2 Parametric dependence and stability of the bifurcating pattern

Before proceeding, we introduce the notation $(\mathcal{M} + \xi)^{-1}\mathcal{K}u_0$ for the set of solutions to the problem $(\mathcal{M} + \xi)y = \mathcal{K}u_0$. Here, $\xi \in \mathbb{C}$ is arbitrary and the given boundary conditions for y apply. In particular, $\mathcal{M}^{-1}\mathcal{K}u_0$ is well defined because $0 \notin \sigma_p(\mathcal{M})$ by earlier assumptions. The only values of ξ requiring special attention are, in fact, the isolated values $\{-\mu_j\} = \sigma_p(-\mathcal{M})$, for which the solution set is either empty or a nontrivial affine subspace; this depends on whether or not $\mathcal{K}u_0 \in \text{range}(\mathcal{M} - \mu_j)$ and thus on model particulars. We also define the function

$$a : \mathbb{C} \setminus \sigma_p(-\mathcal{M}) \rightarrow \mathbb{C},$$

$$a(\xi; \Lambda_0) = P_0^a(f_0 u_0 (\mathcal{M} + \xi)^{-1} \mathcal{K} u_0), \quad (3.5)$$

which plays a crucial role below. Note that $a(\xi; \Lambda_0)$ depends only implicitly on Λ_0 through the eigenfunction u_0 ; we will suppress this dependence when no confusion can arise.

All equilibria $(x_0, y) \in \mathbb{R} \times \mathbb{X}_v$ of (3.4) satisfy, at leading order in ε , the system

$$\begin{aligned} x_0 [\Lambda_0 - P_0^a(f_0 u_0 y)] &= 0, \\ x_0 \mathcal{K} u_0 - \mathcal{M} y &= 0. \end{aligned} \quad (3.6)$$

Assuming that

$$a(0) = P_0^a(f_0 u_0 \mathcal{M}^{-1} \mathcal{K} u_0) \neq 0, \quad (3.7)$$

(3.6) has the isolated solutions

$$\begin{aligned} (x_0^0, y^0) &= (0, 0), \\ (x_0^*, y^*) &= \frac{\Lambda_0}{a(0)} (1, \mathcal{M}^{-1} \mathcal{K} u_0). \end{aligned} \quad (3.8)$$

Condition (3.7) ensures that the bifurcating branch of equilibria grows linearly in the direction $(1, \mathcal{M}^{-1} \mathcal{K} u_0)_{\lambda_0=0}$, local to the bifurcation point ($\Lambda_0 \ll 1$); see Theorem 1.7 and 1.18 in [28]. If $\mathbb{X}_{u,0}$ evolves slowly with Λ_0 as in our earlier remark, then the branch evolves approximately linearly also for $\mathcal{O}(1)$ values of Λ_0 .

The spectral stability problem for (x_0^*, y^*) is a parametric ODE–PDE problem,

$$\begin{aligned} \xi \bar{x}_0 &= -x_0^* P_0^a(f_0 u_0 \bar{y}), \\ (\mathcal{M} + \xi) \bar{y} &= \bar{x}_0 \mathcal{K} u_0, \end{aligned} \quad (3.9)$$

involving the eigenfunction $(\bar{x}_0, \bar{y}(z))$, the eigenvalue $\xi \in \mathbb{C}$ and inherited boundary conditions for $\bar{y}$. Solving the second equation for $\bar{y}$ and substituting into the first one, we derive the associated algebraic equation for ξ dictating the spectral stability properties of the bifurcating branch,

$$\xi a(0) + \Lambda_0 a(\xi) = 0 \quad (3.10)$$

or, equivalently,

$$\left(1 - \frac{a(\xi) - a(0)}{a(\xi)}\right) \xi = -\Lambda_0. \quad (3.11)$$

If $\mathbb{X}_u$ is a Hilbert space, then $P_0^a = \langle \cdot, \hat{u}_0 \rangle$ and

$$a(\xi) = \langle f_0 u_0 (\mathcal{M} + \xi)^{-1} \mathcal{K} u_0, \hat{u}_0 \rangle. \quad (3.12)$$

This last formula will be central to our work in the next sections. Remarkably, it represents a formulation of the stability problem for the small pattern solely in terms of information on the background state that the pattern emerges from. Indeed, both u_0 and $\hat{u}_0$ relate to the stability problem for that state, and f_0 is the nonlinearity coefficient evaluated at it. Generally, $a(\xi)$ will reflect the infinite-dimensional character of the problem, as it will typically be a transcendental function of ξ and not a polynomial. As will become evident through our treatment of the phytoplankton model, this will allow for richer post-bifurcation dynamics which the one-dimensional center manifold reduction necessarily misses. Note, finally, that $a(\xi)$ can still depend implicitly on Λ_0 through u_0 as per our earlier remark.

3.3 Formation and fate of phytoplankton colonies

We clarify the process laid out above by applying it to a rescaled and dimensionless version of a phytoplankton–nutrient model [78, 176, 177],

$$\begin{aligned} \begin{bmatrix} p \\ n \end{bmatrix}_t = & \begin{bmatrix} \varepsilon \partial_{zz} - 2\sqrt{\varepsilon v} \partial_z + h(z) - \ell & 0 \\ \varepsilon \ell^{-1} h(z) & \varepsilon \partial_{zz} \end{bmatrix} \begin{bmatrix} p \\ n \end{bmatrix} \\ & - \begin{bmatrix} 1 \\ \varepsilon \ell^{-1} \end{bmatrix} (h(z) - \mu(z, p, n)) p \end{aligned} \quad (3.13)$$

with associated boundary conditions

$$\begin{aligned} (\varepsilon p_z - 2\sqrt{\varepsilon v} p)|_{z=0,1} &= 0, \\ n_z(0) &= n(1) = 0. \end{aligned}$$

Table 3.1 summarizes the correspondence between this model and the general system in Section 3.1. Appendix C shows the nondimensionalization of the original phytoplankton–nutrient model that was used to obtain (3.13).

Here, $z \in [0, 1]$ measures rescaled depth from top to bottom, p phytoplankton concentration and n nutrient deviation from a constant and spatially uniform profile attained for $p = 0$. The function h models growth conditions at maximum nutrient concentration (when there is zero deviation),

$$h(z) = \frac{1}{\eta_H + 1} \frac{1}{1 + j_H e^{\kappa z}},$$

so that growth decreases with depth due to light absorption. The nonlinear factor μ is

$$\mu = \frac{1-n}{n_H + 1 - n} \frac{j}{j_H + j},$$

with η_H and j_H dimensionless constants and j the rescaled light intensity at depth z ,

$$j = \exp \left(-\kappa z - r \int_0^z p(s, \tau) ds \right).$$

The dimensionless constants κ and r measure water turbidity and the specific light absorption coefficient of phytoplankton. It is straightforward to verify that the nonlinearity $(\mu - h)p$, modeling nutrient uptake in the water column, is proportional to both n and p as in (3.1).

Section 3.1	Section 3.3
u	p
v	n
$\mathcal{L}$	$\varepsilon \partial_{zz} - 2\sqrt{\varepsilon v} \partial_z + h(z) - \ell$
$\mathcal{M}$	$-\partial_{zz}$
$\mathcal{K}$	$\ell^{-1} h(z)$
$f(z, u, v; \varepsilon) uv$	$(h(z) - \mu(z, p, n))p$
$g(z, u, v; \varepsilon)$	$\ell^{-1} (h(z) - \mu(z, p, n))p$
f_0	$(1 + \eta_H)^{-1} h(z)$
u_j	Es_j (see Appendix)
$\hat{u}_j$	$E^{-1} s_j$
μ_j	$-M_j = -(j + 1/2)^2 \pi^2$
n_j	$\cos(\sqrt{M_j} x).$

Table 3.1: Notation conversion table.

3.3.1 Linear stability

The nature of the bifurcating profile and of its dynamics after the first bifurcation depend strongly on the value of parameter v . This, in turn, is influenced by both physiological properties of plankton and environmental factors. Buoyant plankton ($v \leq 0$) tends to aggregate near the surface, whereas sinking plankton does so at a well-defined depth $z_* > 0$. As v approaches the threshold value $v^* = h(0) - h(1)$, the bloom shifts toward the bottom monotonically ($z_* \uparrow 1$). For $v > v^*$, the bloom occurs *at* the bottom ($z_* = 1$) [177]. Depending on

their localization properties, these *stationary* blooms are known as *surface scums* (SS), *deep chlorophyll maxima* (DCM) or *benthic layers* (BL), respectively, and correspond to equilibria of the model.

This state of affairs is reflected in the eigenvalues $\{\lambda_j\}$ and eigenfunctions $\{p_j\}$ of the stability problem for the trivial steady state. Asymptotic expressions for these have been derived elsewhere [177]. At leading order in ε , the primary eigenvalue λ_0 reads

$$\lambda_0 = \begin{cases} \lambda_{BL} & = h(1) - \ell + \mathcal{O}(\varepsilon^{\frac{1}{2}}), & v > v^*, \\ \lambda_{DCM} & = h(0) - \ell - v - \mathcal{O}(\varepsilon^{\frac{1}{3}}), & v < v^*, \end{cases}$$

while the higher-order eigenvalues are given by

$$\lambda_{j \geq 2} = h(0) - \ell - v - \mathcal{O}(\varepsilon^{1/3}),$$

i.e. the eigenvalues $\lambda_{j \geq 2}$ are a mere $\mathcal{O}(\varepsilon^{1/3})$ distance away from λ_{DCM} . The value of v relative to v^* determines the nature of the primary pair (λ_0, p_0) and, therefore, also the nature of the bifurcating profile as the trivial state loses stability.

The eigenvalue set $\{\mu_j\}_j$ is parameter-independent and negative. For this model, both $\{\mu_j\}$ and the associated eigenfunctions $\{n_j\}$ are explicitly computable, see Table 3.1. We finally recall that $P_0^a = \langle \cdot, \hat{p}_0 \rangle$, with $\hat{p}_0$ the dual of p_0 .

3.3.2 Evolution of DCM profiles

For $0 < v < v^*$, a stable DCM branch emerges at $\lambda_0 = 0$ through a trans-critical bifurcation and subsequently undergoes a secondary, destabilizing Hopf bifurcation already for $\lambda_0 = \mathcal{O}(\varepsilon)$ [177]. Both the primary and the secondary bifurcations have been analyzed, and a weakly nonlinear stability analysis was performed by recasting (3.1) as an infinite-dimensional ODE system [176]. In this section, we repeat that analysis along the lines of Section 3.2, so as to benchmark the method detailed there, to compactly recover the oscillatory DCM destabilization mechanism and to further familiarize the reader with the model and the method.

Before delving into details, we compute the function $a(\xi; \Lambda_0)$ introduced in (3.5). Here, this function takes the form (cf. (3.12))

$$a(\xi) = \frac{1}{\ell} \langle f_0 p_0 (\mathcal{M} + \xi)^{-1} (h p_0), \hat{p}_0 \rangle, \quad (3.14)$$

where $(\mathcal{M} + \xi)^{-1}$ is the solution operator to

$$-n_{zz} + \xi n = w(z), \quad n_z(0) = n(1) = 0, \quad (3.15)$$

and with w arbitrary. The solution is

$$((\mathcal{M} + \xi)^{-1}w)(z) = \int_0^1 G(z, s; \xi)w(s)ds,$$

with G the associated Green's function,

$$G(z, s; \xi) = \frac{\cosh(\sqrt{\xi} \min(z, s)) \sinh(\sqrt{\xi}(1 - \max(z, s)))}{\sqrt{\xi} \cosh \sqrt{\xi}}. \quad (3.16)$$

The function $a(\xi; \Lambda_0)$ becomes, then,

$$a(\xi; \Lambda_0) = \frac{1}{\ell} \iint_{[0,1]^2} f_0(r) \hat{p}_0(r) p_0(r) G(r, s; \xi) h(s) p_0(s) ds dr. \quad (3.17)$$

We can readily estimate the integral asymptotically by noting that p_0 and $\hat{p}_0 p_0$ are strongly localized [176]. Through an application of Laplace's method, the localization of p_0 about z_* implies the leading order result

$$\int_0^1 G(r, s; \xi) h(s) p_0(s) ds = G(r, z_*; \xi) h(z_*) \|p_0\|_1;$$

see also [176, Section 3]. By the same token, using that $\hat{p}_0 p_0$ is localized about zero, as well as the identities $\int_0^1 \hat{p}_0 p_0 = 1$ and $h(z_*) = \ell$, we find

$$a(\xi; \Lambda_0) = G(0, z_*; \xi) f_0(0) \|p_0\|_1,$$

see also [176]. This is the desired formula for $a(\xi; \Lambda_0)$, with

$$G(0, z_*; \xi) = \frac{\sinh(\sqrt{\xi}(1 - z_*))}{\sqrt{\xi} \cosh \sqrt{\xi}}.$$

Note that, for $\xi = 0$,

$$G(z, s; 0) = 1 - \max(z, s)$$

and hence also

$$a(0; \Lambda_0) = f_0(0) \|p_0\|_1 (1 - z_*) = \lim_{\xi \downarrow 0} a(\xi; \Lambda_0).$$

Combining this last equation with (3.8), we obtain a leading order result for x_0^* . Recalling, additionally, that the remainder x_r is higher-order by the slaving

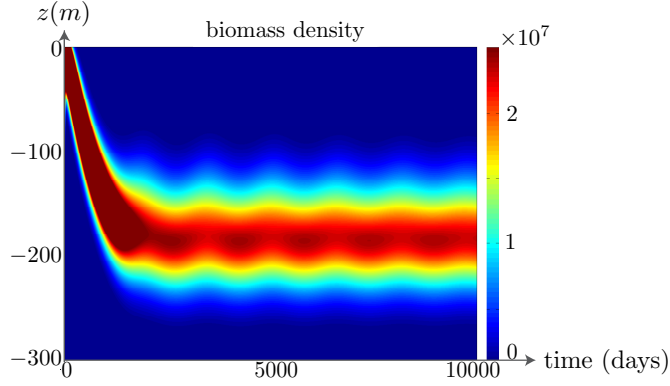


Figure 3.1: Numerical simulation of (3.13) showcasing the growth of an oscillatory DCM from an initial perturbation. Here, depth is dimensional and the parameters are chosen in the DCM regime: $\varepsilon = 9 \cdot 10^{-5}$, $v = 0.063$, $\ell = 0.25$, $\eta_H = 0.4$, $j_H = 0.033$, $\kappa = 4$ and $r = 0.65$. The period of the oscillation is of the order of years, correlating well with the longest diffusive timescale. For the values of the dimensional parameters associated with the nondimensional parameters, see Appendix C.

relation (3.3), we recover the leading order result [176, Eq. (4.9)] describing the nontrivial plankton profile for our phytoplankton-nutrient model,

$$p^*(z) = \varepsilon x^*(z) = \frac{\varepsilon \Lambda_0}{f_0(0)(1 - z_*)} \frac{p_0(z)}{\|p_0\|_1}.$$

The biomass contained in that profile is $\int_0^1 p^* dz = \varepsilon \Lambda_0 / (f_0(0)(1 - z_*))$, which also matches the prior result [176, Eq. (1.20)]. The stability problem (3.10) for p^* reads

$$\xi(1 - z_*) + \Lambda_0 \frac{\sinh(\sqrt{\xi}(1 - z_*))}{\sqrt{\xi} \cosh \sqrt{\xi}} = 0 \quad (3.18)$$

which, in turn, is identical to [176, Eq. (4.28)]. An analysis of this equation establishes the destabilization of the bifurcating pattern through a secondary, Hopf bifurcation [176]. This behavior is beautifully captured in Figure 3.1, where a localized structure is shown to develop at a depth of 120 – 220 meters in a oceanic layer with a depth of 300 meter.

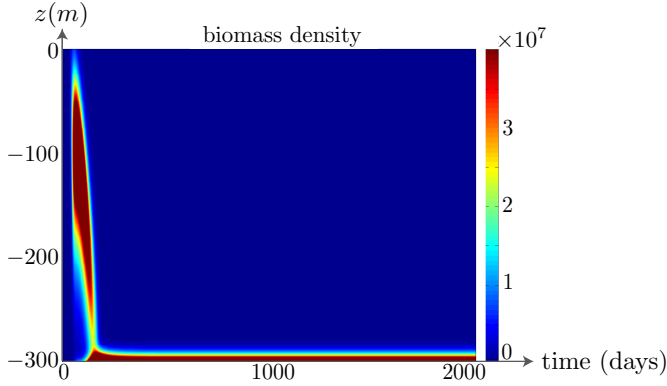


Figure 3.2: Numerical simulation of (3.13), showcasing the growth of a stationary benthic layer from an initial perturbation. The parameters here are chosen in the benthic layer regime ($\varepsilon = 9 \cdot 10^{-5}$, $v = 0.56$, $\ell = 0.25$, $\eta_H = 0.4$, $j_H = 0.033$, $\kappa = 4$, and $r = 0.65$). For the values of the dimensional parameters associated with the nondimensional parameters, see Appendix C.

3.4 Short-term evolution of bifurcating benthic layers

As we mentioned in the previous section, the bifurcating profile and its dynamics depend on the value of v . An elevated sinking speed, decreased production rate or shallower top oceanic layers increase the value of v , potentially changing the profile's qualitative properties. For $v > v^*$, in particular, the localized peak of the eigenfunction migrates to the bottom of the layer ($z = 1$) [177], and the corresponding, primary eigenvalue reads $\lambda_0 = h(1) - \ell + \mathcal{O}(\sqrt{\varepsilon})$. As a result, the small pattern developing past $\lambda_0 = 0$ is shaped as a *benthic layer* (BL), see Figure 3.2.

In this part, we formulate and investigate the stability problem for small patterns of BL-type. Our analysis roughly proceeds as in the last section, but the asymptotic estimates are technically more involved and largely deferred to the Appendix. We find that, contrary to the DCM case, the presence of slow spatial processes does *not* lead to destabilization of BL-type patterns in the regime we examine. Such patterns can and do develop transient oscillatory behavior, evidenced by the complexification of eigenvalues in their spectrum. Nevertheless, the oscillations here remain damped, unlike the sustained oscillations undergone by DCM patterns; eigenvalues cannot escape the left-half complex plane and, accordingly, BL patterns remain stable.

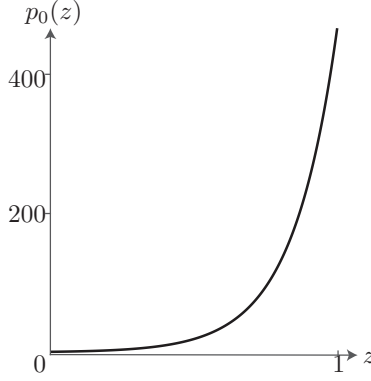


Figure 3.3: Eigenfunction profile p_0 in the case $v > v^*$.

3.4.1 Bifurcating profile

The primary eigenfunction p_0 can be approximated using the WKB method [76], see also Section 7.2 in [176]. First, the Liouville transform $p_0(z) = E(z)s_0(z) = e^{\sqrt{v/\varepsilon}z}s_0(z)$ results in a self-adjoint formulation of the eigenvalue problem, by removing the advection term:

$$\begin{aligned} \varepsilon(s_0)_z - (\ell + v - h(z) + \lambda_0)s_0 &= 0, \\ (s_0)_z(z) - \sqrt{v/\varepsilon}s_0(z)|_{z=0,1} &= 0. \end{aligned} \quad (3.19)$$

The WKB method yields, at leading order,

$$\begin{aligned} s_0(z) &= \frac{\sqrt{2v}}{\varepsilon^{1/4}Q_0^{1/4}(z)} e^{-\int_z^1 \sqrt{Q_0(s)/\varepsilon} ds}, \\ Q_0(z) &= h(1) - h(x) + v + \mathcal{O}(\sqrt{\varepsilon}), \end{aligned} \quad (3.20)$$

where we have normalized $s_0(z)$ under the $L^2(0, 1)$ norm. This profile is depicted in Figure 3.3 for the parameter values of Figure 3.2 but with $\varepsilon = 9 \cdot 10^{-3}$.

The function $a(\xi; \Lambda_0)$, appearing in the stability problem (3.10)–(3.11) is as reported in (3.14). Note that the inner product now corresponds to a projection on the benthic layer profile p_0 . Green's function (3.16) also remains unchanged, since (3.15) does not depend on v . Furthermore, the dual of p_0 assumes the form $\hat{p}_0 = E^{-1}s_0$, due to the self-adjointness of (3.19). According to (3.8), the nontrivial branch of equilibria bifurcating at $\Lambda_0 = 0$ is

$$(x_0^*(z), y^*(z)) = \frac{\Lambda_0}{a(0; \Lambda_0)} \left(1, \frac{1}{\ell} \int_0^1 p_0(s)G(z, s; 0)h(s)ds \right);$$

note, here, that p_0 depends on Λ_0 . Upon bifurcation, the stationary profile of the planktonic component develops in the shape of p_0 , shown in Figure 3.3, and amplitude growth is parametrized by Λ_0 .

3.4.2 Stability

As in Section 3.3.1, the stability properties of the bifurcating profile are governed by (3.10), with $a(\xi; \Lambda_0)$ given in (3.14). However, our asymptotic analysis here is much more involved since, in contrast to that section, it must take into account higher-order terms. A first indication of that is supported by a brief study of the limit $z_* \uparrow 1$ of the DCM case. In that limit, the deep chlorophyll maximum sinks and becomes a benthic layer, but the leading order problem (3.18) becomes trivial, indicating the need of higher-order approximations. In what follows, we work out the stability problem, referring the reader to Appendix A for computational details.

First, since p_0 is strongly localized at $z = 1$, one may estimate $a(\xi)$ by Laplace's method, cf. Section 3.3.2. Leading order asymptotics yield

$$a(\xi) = \varepsilon^{3/4} \frac{e^{\sqrt{v/\varepsilon}} h(1) f_0(1)}{4\sqrt{2}\ell v^{3/4}} + \mathcal{O}(\varepsilon^{5/4}),$$

which implies, as it does not depend on ξ , $a(\xi; \Lambda_0) = a(0; \Lambda_0)$; see Appendix A. With this leading order result, one only captures the single eigenvalue $\xi = -\Lambda_0$ from (3.11). Including the next order term, we find

$$1 - \frac{a(\xi) - a(0)}{a(\xi)} = 1 + \sqrt{\varepsilon} \frac{\sqrt{\xi} \tanh(\sqrt{\xi})}{\sqrt{v}}$$

and (3.11) becomes

$$\left(1 + \sqrt{\varepsilon} \frac{\sqrt{\xi} \tanh(\sqrt{\xi})}{\sqrt{v}}\right) \xi = -\Lambda_0, \quad (3.21)$$

which determines infinitely many other eigenvalues $\xi \in \mathbb{C}$.

We proceed with studying (3.21) in a way that resembles Section 4.4 in [176]. We set $\sqrt{\xi} = \mu = \mu_R + i\mu_I$ and restrict $\arg(\mu)$ to lie in $[0, \pi/2]$, because eigenvalues come in complex conjugate pairs. The stability equation for μ becomes,

$$p(\mu) = -\mu^2 - \sqrt{\frac{\varepsilon}{v}} \mu^3 \tanh(\mu) = \Lambda_0 > 0. \quad (3.22)$$

First, we observe that there are no solutions $\xi \in \mathbb{R}_{>0}$ (equivalently, $\mu > 0$), because p and Λ_0 differ in sign; see Figure 3.4 for an illustration. As $\Lambda_0 \downarrow 0$,

the (real) eigenvalues ξ remain in $\mathcal{O}(\sqrt{\varepsilon})$ neighborhoods of $-\Lambda_0$ and $\sigma_p(-\mathcal{M})$. This is also supported by Figure 3.4, where we have plotted $\{p(\sqrt{\xi})|\xi \in \mathbb{R}_{<0}\}$ (blue curve); real solutions correspond to intersections between that curve and the horizontal at height Λ_0 . The curve approaches vertical asymptotes at the elements of $\sigma_p(-\mathcal{M})$, and becomes unbounded. As $\varepsilon \downarrow 0$, the approach becomes steeper and the intersections of p with the horizontal axis limit to $\{0\} \cup \sigma_p(-\mathcal{M})$.

As Λ_0 increases, the first few eigenvalues complexify and the story takes a turn. We begin by noting the existence of a local maximum for the first curve branch, occurring for some $\xi \in (-\mu_1, 0)$; see Figure 3.4. As the horizontal at height Λ_0 increases, the largest two eigenvalues (intersections) approach each other, collide and develop a nonzero imaginary part; they form a conjugate pair. We have plotted the real part of that pair in red in Figure 3.4. As Λ_0 increases further, the horizontal line at height Λ_0 encounters the local minimum of the second branch. Here, the pair reconnects and splits into two negative eigenvalues, again indicated in blue. The largest of these approaches $-\mu_1$ asymptotically, while the other collides with the third eigenvalue and the process restarts. The smaller the value of ε , the larger the number of these maxima and hence the more eigenvalues are complexified subsequently as Λ_0 increases. For each ε , however, there is a global maximum of p , where the last complex pair is formed, which never returns to the real line.

Importantly, the conjugate pairs thus created do not cross into the right-half complex plane, because (3.22) admits no imaginary solutions. This is supported by Figure 3.4, where the real part of each conjugate pair can be seen to move away from the imaginary axis, as Λ_0 increases. To prove it, we write $\xi = i\hat{\xi} \in i\mathbb{R}_{>0}$ and note that $\mu = \hat{\mu}(1+i)$, for some $\hat{\mu} \in \mathbb{R}_{>0}$. Splitting real and imaginary parts in (3.22) and substituting from one into the other, we find

$$2\hat{\mu}^2 \left(-1 + \sqrt{\frac{\varepsilon}{v}} \hat{\mu} \frac{\sin(2\hat{\mu})}{\sinh^2(\hat{\mu}) + \cos^2(\hat{\mu})} \right) = \Lambda_0. \quad (3.23)$$

No solutions exist because, again, the two sides differ in sign. Since

$$\left| \hat{\mu} \frac{\sin(2\hat{\mu})}{\sinh^2(\hat{\mu}) + \cos^2(\hat{\mu})} \right| < 1,$$

the left member of (3.23) is in $(-1 - \sqrt{\varepsilon/v}, -1 + \sqrt{\varepsilon/v}) \subset \mathbb{R}_{<0}$, for ε small. As we consider $\Lambda_0 > 0$, only there exists no nontrivial solution $\hat{\mu}$ to (3.23), and hence no purely imaginary eigenvalues ξ of (3.21). The real parts of the complex eigenvalues thus never change sign.

Since the spectrum of the stability problem (3.21) remains in the left-half complex plane, we conclude that the benthic layer remains stable for $\mathcal{O}(1)$,

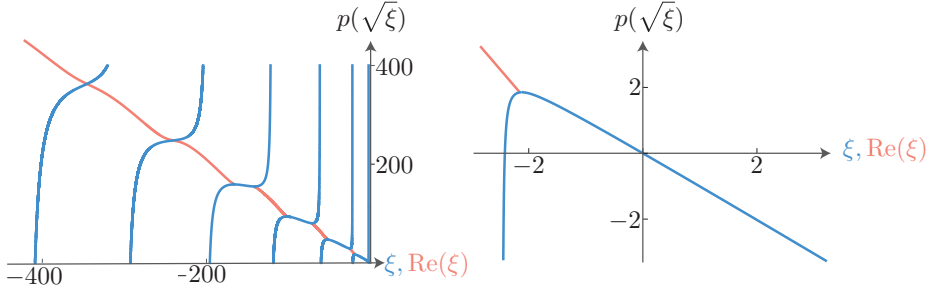


Figure 3.4: Left: In blue, the function $p(\sqrt{\xi})$ for $\xi \in \mathbb{R}$ in a neighborhood of the origin. Red: the function $p(\sqrt{\xi})$, where the argument is no longer purely imaginary, so that $p(\sqrt{\xi})$ is a function over the complex plane. The red curve is the projection of this function onto the $\Im\sqrt{\xi} = 0$ plane. Here, $\sqrt{\varepsilon}/v = 10^{-2}$. Right: In blue, the function $p(\sqrt{\xi})$ for $\xi < 0$ in a neighborhood of the origin. Red: the function $p(\sqrt{\xi})$, where the argument is no longer purely imaginary, so that $p(\sqrt{\xi})$ is a function over the complex plane. The red curve is the projection of this function onto the $\Im\sqrt{\xi} = 0$ plane. Here, $\sqrt{\varepsilon}/v = 10^{-2}$.

positive values of Λ_0 . The reader should contrast this behavior to that of deep chlorophyll maxima which, as we mentioned, undergo oscillatory destabilization soon after they bifurcate. The difference between these two patterns is underlined by numerical simulations, such as those of Figures 3.1 and 3.2. Numerically, one solely observes stationary BL profiles. Stationary DCM profiles are also present, but can only be detected in a targeted manner as they only exist in an asymptotically small parametric region.

In the region $v \approx v^*$, one expects the system dynamics to exhibit interplay between BL and DCM patterns. In that region, the two first eigenvalues cross the imaginary axis in close succession. This is what was referred to as a codimension 2 bifurcation in earlier work [176], where the existence of such patterns was hypothesized but not proved. Figure 3.5 demonstrates what is possibly one such pattern, where a rather shallow DCM and a BL alternate in a periodic fashion. This simulation serves as numeric indication of the existence and stability of such mixed patterns in (3.13). At the same time, it very possibly illuminates the wide chasm separating nonlinear reality, on one hand, from attempts to explore it through linear analysis on the other. As we briefly mentioned in the Introduction, we expect that the method developed here will prove helpful in covering some of that ground. At present, we defer all analysis to future work.

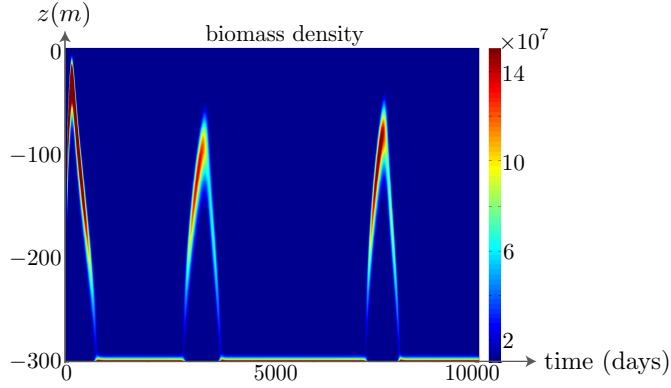


Figure 3.5: Numerical simulation close to the codimension 2 bifurcation showcasing the appearance of a periodic state that interpolates a DCM and a BL. The specific parameters values for this simulation are $\varepsilon = 9 \cdot 10^{-5}$, $v = 0.32$, $\ell = 0.25$, $\eta_H = 0.3$, $j_H = 0.033$, $\kappa = 4$ and $r = 0.65$. For the values of the dimensional parameters associated with the nondimensional parameters, see Appendix C.

3.5 Conclusions

In this chapter, we considered the evolution of small amplitude patterns bifurcating from a trivial state in evolutionary PDE systems. In that direction, we specifically developed a novel analytical framework to study their dynamics beyond the range of applicability of classical, one-dimensional, center manifold reduction. Our main insight is that, in general PDE systems such as (3.1), classical reduction can and must be extended to capture dynamically significant behavior. The result of that process is the reduced model (3.4), comprised of a nonlinear ODE and a linear PDE. The two govern, respectively, the amplitude of the emerging pattern and the slow spatial processes mentioned in the title of this communication. The coupling between them is strong and describes accurately the interactions between pattern and ambient environment.

Using that framework, we next examined the infinite-dimensional eigenvalue problem determining pattern stability. We were able to encapsulate that in a transcendental equation that elegantly conflates information from the background state and the generator of the spatial processes. This analytical result is expressed in (3.10)–(3.12), and its solutions correspond to eigenvalues of the stability problem. As such, it extends, streamlines and simplifies similar results where the infinite-dimensional system was used to work with, instead of the ODE–PDE

formulation, see [176] and Chapter 2.

Finally, we applied our general method to a specific example describing the interaction of phytoplankton and nutrient in a water column [78, 177, 176]. This enabled us to recover swiftly the onset of oscillations in *deep chlorophyll maxima*, a phenomenon previously observed and simulated [78] as well as analyzed by less elaborate methods [176]. Moreover, our method allowed us to extend earlier insights [78, 176, 177] by considering the more degenerate dynamics of *benthic layers*.

3.6 Acknowledgements

We wish to thank Prof. Huib de Swart and Brianna Liu (University of Utrecht, IMAU) for generously providing the simulator for (3.1). LS acknowledges the support of NWO through the *Nonlinear Dynamics in Natural Systems* (NDNS⁺) cluster.

Appendices

A Approximation of integrals with a localized function

The primary eigenfunction $p_0(z)$ associated with a benthic layer has a very narrow, large amplitude at $z = 1$, see Figure 3.3. In this appendix, we will write p_0 as,

$$p_0(z) = A(z)e^{-\frac{1}{\sqrt{\varepsilon}}H(z)} \quad (3.24)$$

with $H(z) = \int_z^1 \sqrt{Q(s)}ds - \sqrt{v}z$ and $A(z) = \sqrt{2v\varepsilon}^{-1/4}Q(z)^{-1/4}$.

We use the localized structure of p_0 to our advantage in approximating integrals of the form

$$\int_0^x f(z)p_0(z)dz = \int_0^x F(z)e^{-\frac{1}{\sqrt{\varepsilon}}H(z)}, \quad (3.25)$$

where $f(z)$ is (with a slight abuse of notation) any real, continuous function and $F(z) = f(z)A(z)$. The technique used for approximation is called *Laplace's method* [174, 76] and was applied repeatedly in earlier work on phytoplankton patterns [176]. The idea behind this method is to evaluate an integral with an exponentially decaying factor only at its maximum, because the error is exponentially small. In our case, the exponential in (3.25) is maximal where $H(z)$ is minimal. $H(z)$ is monotonically decreasing, hence the minimum of $H(z)$ for $z \in [0, x]$ is at $z = x$. We Taylor expand,

$$\begin{aligned} H(z) &= H(x) + \sum_{n \geq 0} a_n(z-x)^{n+1}, \\ F(z) &= \sum_{n \geq 0} b_n(z-x)^{n+\alpha-1}, \end{aligned} \quad (3.26)$$

with $\alpha > 0$ and compute $a_0 = -\sqrt{Q(x)} - \sqrt{v}$ and $a_1 = -\frac{1}{4} \frac{Q'(x)}{2\sqrt{Q(x)}}$. Laplace's

method yields, up to $\mathcal{O}(\varepsilon^{\frac{\alpha}{2}+1})$ corrections,

$$\int_0^x F(z) e^{-\frac{H(z)}{\sqrt{\varepsilon}}} dz = -e^{-\frac{H(x)}{\sqrt{\varepsilon}}} \varepsilon^{\frac{\alpha}{2}} \left(\Gamma(\alpha) \frac{b_0}{a_0^\alpha} + \sqrt{\varepsilon} \frac{\Gamma(\alpha+1)}{a_0^{\alpha+1}} \left[b_1 - \frac{(\alpha+1)a_1 b_0}{a_0} \right] \right), \quad (3.27)$$

as $\varepsilon \rightarrow 0$ [174, 76]. Note the Gamma function $\Gamma(n) = (n-1)!$ for natural numbers n .

B Approximation of the eigenvalue function

The eigenvalue function $a(\xi; \Lambda_0)$ is defined in equation (3.5),

$$a(\xi; \Lambda_0) = \frac{1}{\ell} \left\langle f_0 p_0 \int_0^1 G(z, s; \xi) h(s) p_0(s) ds, \hat{p}_0 \right\rangle,$$

but due to the definition of $G(z, s; \xi)$, we need to split the inner integral into separate integrals taking care of $\min(z, s)$ and $\max(z, s)$. After that, we use Laplace's method to approximate $\int_0^1 G(z, s; \xi) h(s) p_0(s) ds$, and then perform it once more to find $a(\xi)$. The leading order result is:

$$a(\xi) = \varepsilon^{3/4} \frac{e^{v/\varepsilon} h(1) f_0(1)}{4\sqrt{2}\ell v^{3/4}}. \quad (3.28)$$

Note that this leading order term does not depend on ξ , hence $a(0)$ has the same leading order term.

For the stability equation (3.11), we therefore consider the difference

$$\begin{aligned} \ell(a(\xi) - a(0)) &= \left\langle f_0 p_0 \int_0^1 G(z, s; \xi) h p_0 ds, \hat{p}_0 \right\rangle \\ &\quad - \left\langle f_0 p_0 \int_0^1 G(z, s; 0) h p_0 ds, \hat{p}_0 \right\rangle \\ &= \int_0^1 f_0 s_0^2 \int_0^1 h p_0 [G(z, s; \xi) - G(z, s; 0)] ds dz \end{aligned} \quad (3.29)$$

For $\xi \rightarrow 0$, the Green's function becomes $G(z, s; 0) = \lim_{\xi \rightarrow 0} G(z, s; \xi) = 1 - \max(z, s)$.

$$\begin{aligned}
 & \int_0^1 f_0 s_0^2 \int_0^1 G(1, 1 - s + z; \xi) h p_0 ds dz \\
 & - \int_0^1 f_0 s_0^2 \int_0^1 G(1, 1 - s + z; 0) h p_0 ds dz \\
 & + \int_0^1 f_0 s_0^2 \int_0^1 (G(-z, s; \xi) - G(-z, s; 0)) h p_0 ds dz,
 \end{aligned}$$

because $G(1, 1 - s + z; \xi)$ is zero for $z \leq s \leq 1$ and $\min(-z, s)$ and $\max(-z, s)$ do not change for $0 \leq s, z \leq 1$. We shall evaluate separately for every Green's function. Define

$$\begin{aligned}
 I_{1,i} &= \int_0^1 G(1, 1 - s + z; i) h(s) p_0(s) ds, \\
 I_{2,i} &= \int_0^1 G(-z, s; j) h(s) p_0(s) ds.
 \end{aligned}$$

with $i \in \{\xi, 0\}$. Integrals $I_{1,i}$ and $I_{2,i}$ are of the form (3.25) and we use the following table to approximate them with Laplace's method.

	α	b_0	b_1
$I_{1,\xi}$	2	$\sqrt{\xi} \frac{h(z)}{Q^{1/4}(z)}$	$\frac{h(z)Q'(z)}{4Q^{5/4}(z)} - \frac{h'(z)}{Q^{1/4}(z)}$
$I_{1,0}$	1	$\frac{h(z)}{Q^{1/4}(z)}$	—
$I_{2,\xi}$	2	$-\sqrt{\xi} \frac{h(1)}{v^{1/4}}$	$-\sqrt{\xi} \frac{h'(1)h(1)}{4v^{5/4} - v^{1/4}}$
$I_{2,0}$	1	$\frac{h(1)}{v^{1/4}}$	—

The higher order coefficients of $I_{1,0}$ and $I_{2,0}$ are not needed for the approximation, compared to $I_{1,\xi}$ and $I_{2,\xi}$ (compare $\alpha = 1$ versus $\alpha = 2$). Substituting the Taylor coefficients into approximation (3.27) and combining terms yields

$$\begin{aligned}
 \ell(a(\xi) - a(0)) &\rightarrow \frac{1}{2} \sqrt{2}(\varepsilon v)^{\frac{1}{4}} h(1) e^{\sqrt{\frac{v}{\varepsilon}}} \\
 &\quad \int_0^1 \frac{f_0(z)}{\sqrt{Q(z)}} e^{-\frac{2}{\sqrt{\varepsilon}} \int_z^1 \sqrt{Q(s)} ds} \left(1 - \frac{\cosh(\sqrt{\xi} z)}{\cosh(\sqrt{\xi})} \right) dz
 \end{aligned} \tag{3.30}$$

which is a second order Laplace approximation. The integral over z , which is left, is not of the form (3.25), as the exponential is now

$$e^{-\frac{2}{\sqrt{\varepsilon}} \int_z^1 \sqrt{Q(s)} ds}.$$

The factor $\int_z^1 \sqrt{Q(s)} ds$ is also monotonically decreasing, and hence we can estimate (3.30) at $z = 1$. Using Taylor approximations, we find $\alpha = 2$, and Laplace's method yields

$$\begin{aligned} \ell(a(\xi) - a(0)) &\rightarrow \\ & - \varepsilon^{\frac{5}{4}} e^{\sqrt{\frac{\gamma}{\varepsilon}}} \frac{(h(1))^2 \eta_H}{4\sqrt{2}(1 + \eta_H) \ell v^{3/4}} \sqrt{\xi} \tanh(\sqrt{\xi}). \end{aligned} \quad (3.31)$$

C Nondimensionalization

The system analyzed in sections 3.3 and 3.4 is a nondimensionalized version of a phytoplankton-nutrient model as stated in [78] and [177],

$$\begin{aligned} W_{\hat{t}} &= DW_{\hat{z}\hat{z}} - VW_{\hat{z}} + \left[\hat{\mu}P(L, N) - \hat{\ell} \right] W, \\ N_{\hat{t}} &= DN_{\hat{z}\hat{z}} - \alpha \hat{\mu}P(L, N)W, \end{aligned} \quad (3.32)$$

with

$$\begin{aligned} L(\hat{z}, \hat{t}) &= L_I e^{-K_{\text{bg}} \hat{z} - R \int_0^{\hat{z}} W(\xi, \hat{t}) d\xi}, \\ P(L, N) &= \frac{LN}{(L + L_H)(N + N_H)}. \end{aligned} \quad (3.33)$$

The coordinates $\hat{z}$ and $\hat{t}$ represent depth – $\hat{z} \in (0, z_B)$ and time. The system (3.32) is subject to boundary conditions,

$$\begin{aligned} DW_{\hat{z}} - VW_{\hat{z}}|_{\hat{z}=0, z_B} &= 0, \\ N_{\hat{z}}|_{\hat{z}=0} &= 0, \\ N|_{\hat{z}=z_B} &= N_B. \end{aligned} \quad (3.34)$$

Here, W and N are the phytoplankton and nutrient concentration in a water column of depth z_B , and the system is assumed to be in a turbulent mixing regime. The parameters V , $\hat{\ell}$, α and $\hat{\mu}$ measure the sinking speed of phytoplankton, the species-specific loss rate, the conversion factor and the maximum specific production rate, respectively. The function L models the light intensity, where L_I is the light intensity at the surface, R is the shading due to plankton and K_{bg} is the light absorption coefficient. Lastly, L_H and N_H are half-saturation constants of light and nutrient, respectively.

The relevant parameter values used in [78] and their units are reported in C.1. By introducing new parameters and coordinates, we rescale system (3.32) to a nondimensional system.

Indicent light intensity	L_I	600	m^2/s
Background turbidity	K_{bg}	0.045	m^{-1}
Absorption coeff. phyto	R	$6 \cdot 10^{-10}$	m^2/cell
Depth	z_B	300	m
Vert. turbulent diffusivity	D	$1.2 \cdot 10^{-5}$	m^2/s
Max. specific growth rate	$\hat{\mu}$	$1.11 \cdot 10^{-4}$	s^{-1}
Half-sat. light	L_H	20	m^2/s
Half-sat. nutrient	N_H	$2.5 \cdot 10^{-2}$	m^{-3}
Specific loss rate	$\hat{\ell}$	$2.78 \cdot 10^{-6}$	s^{-1}
Nutrient content phyto	α	$1 \cdot 10^{-9}$	$\text{mmol}/\text{cell}^3$
Sinking velocity	V	$1.17 \cdot 10^{-5}$	m/s
Bottom nutrient supply	N_B	10	m^{-3}

Table C.1: Dimensional parameters of (3.32) used in [78] for a simulation in which the phytoplankton seems to behave chaotically.

$$\begin{aligned}
 z &= \frac{\hat{z}}{z_B} & \ell &= \frac{\hat{\ell}}{\hat{\mu}}, \\
 t &= \hat{\mu} \hat{t} & v &= \frac{V^2}{4\hat{\mu}D}, \\
 p(z, t) &= \frac{\hat{\ell}\alpha z_B^2}{DN_B} W(\hat{z}, \hat{t}) & \eta_H &= \frac{N_H}{N_B} \\
 n(z, t) &= 1 - \frac{N(\hat{z}, \hat{t})}{N_B} & \kappa &= K_{\text{bg}} z_B, \\
 \varepsilon &= \frac{D}{\hat{\mu} z_B^2} & r &= \frac{RDN_B}{\hat{\ell}\alpha z_B}.
 \end{aligned} \tag{3.35}$$

Note that n rescales N as the offset of nutrient from the maximum at the bottom, N_B . The rescaling transforms systems (3.32) to

$$\begin{aligned}
 p_t &= \varepsilon p_{zz} - 2\sqrt{\varepsilon} p_z + (\mu(z, p, n) - \ell)p, \\
 n_t &= \varepsilon n_{zz} + \varepsilon \ell^{-1} \mu(z, p, n)p.
 \end{aligned} \tag{3.36}$$

with

$$\mu(z, p, n) = \frac{j(1-n)}{(j-j_H)(\eta_H+1-n)}, \quad j = e^{-\kappa z - r \int_0^z p(\xi, t) d\xi}.$$

parameter	Figure 3.1	Figure 3.2	Figure 3.5
L_I	600	600	600
K_{bg}	$1.33 \cdot 10^{-2}$	$1.33 \cdot 10^{-2}$	$1.33 \cdot 10^{-2}$
R	$6 \cdot 10^{-10}$	$6 \cdot 10^{-10}$	$6 \cdot 10^{-10}$
z_B	300	300	300
D	$9 \cdot 10^{-5}$	$9 \cdot 10^{-5}$	$9 \cdot 10^{-5}$
$\hat{\mu}$	$1.11 \cdot 10^{-4}$	$1.11 \cdot 10^{-4}$	$1.11 \cdot 10^{-4}$
L_H	20	20	20
N_H	4	4	3
$\hat{\ell}$	$2.78 \cdot 10^{-6}$	$2.78 \cdot 10^{-6}$	$2.78 \cdot 10^{-6}$
α	$1 \cdot 10^{-9}$	$1 \cdot 10^{-9}$	$1 \cdot 10^{-9}$
V	$1.59 \cdot 10^{-5}$	$4.74 \cdot 10^{-5}$	$3.59 \cdot 10^{-5}$
N_B	10	10	10

Table C.2: Dimensional parameters used in the Figures 3.1, 3.2 and 3.5.

The boundary conditions transform according to (3.35), too.

$$\begin{aligned}
 \varepsilon p_z - 2\sqrt{\varepsilon\nu}p|_{z=0,1} &= 0, \\
 n_z(0) &= 0, \\
 n(1) &= 0.
 \end{aligned}
 \tag{3.37}$$

For the figures 3.1,3.2, 3.5, the dimensional parameters that are used to simulate the model are reported in the table C.2.