A MATHEMATICAL EXPLORATION OF
PHYTOPLANKTON BLOOMS IN THE NORTH ATLANTIC

by

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A dissertation submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Applied Mathematics

Summer 2019

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ACKNOWLEDGEMENTS

I am truly grateful for the unique opportunity to pursue my research interests given to me by my advisors L. Pamela Cook and Matthew J. Oliver. Professor Cook’s expertise in mathematical modeling and Professor Oliver’s expertise in biological oceanography allowed me to conduct my dissertation research in an enjoyable, interdisciplinary topic. My advisors were invaluable in their efforts to supervise my research, scrutinize my results, critique my writing, and help me grow professionally as an applied mathematician. I also want to thank my dissertation committee members Pak-Wing Fok and Richard Braun for taking the time to listen to my research updates and for providing valuable feedback. I would like to give a special thanks to Matthew Shatley of the University of Delaware College of Earth, Ocean, and Environment for providing me with data that allowed me to measure the success of my model. I also want to thank the Department of Mathematical Sciences at the University of Delaware for their world-class mathematical training, opportunities to teach mathematics, and financial support that made this dissertation possible. My thanks to the department includes my classmates who were the best study partners and friends that a graduate student can ask for.

I am also grateful for the support of my family. My graduate career has been the most challenging venture of my life and I would not have succeeded without their love and support.
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ABSTRACT

Phytoplankton are the base of the marine food web. They are also responsible for much of the oxygen we breathe and they remove carbon dioxide from the atmosphere. The cause of seasonal phytoplankton blooms in the ocean is a debated topic. One hypothesis is that blooms are initiated when seasonally changing environmental conditions disrupt the balance in the predator-prey relationship between zooplankton and phytoplankton. This dissertation follows up on this notion with a Nutrient-Phytoplankton-Zooplankton (NPZ) model incorporating diffusion and depth-dependent coefficients. Full spatiotemporal solutions of this coupled reaction-diffusion system are computed. An explanation of the bloom process in this model is presented that involves a saddle point transient equilibrium state. The saddle point bloom process is demonstrated with an ordinary differential equations NPZ model with time dependent forcing to imitate seasonally oscillating solar radiation. This process is illustrated by an animation (movie1_ODE.avi). The details from this analysis inform the bloom process in the reaction-diffusion NPZ model for which the equilibria must be determined computationally. The bloom process in the reaction-diffusion NPZ model is illustrated by another animation (movie2_PDE.avi). The reaction-diffusion NPZ model, incorporated with seasonal solar radiation and mixed layer depth data, simulates blooms with better timing than the ordinary differential equations model but still leaves much to be desired. However, results from models that simulate blooms more accurately show signs of the saddle point bloom process described in this dissertation. The saddle point bloom mechanism described here could be the mechanism by which the seasonal disruption in ecological balance initiates a high-latitude marine phytoplankton bloom, like that in the North Atlantic Ocean.
Chapter 1

INTRODUCTION

1.1 The Role of Plankton

Plankton play a vital role in the biology of the ocean as well as in the chemistry of the atmosphere. Phytoplankton are the base of the marine food web [1]. They are responsible for much of the oxygen in the atmosphere [2]. As photosynthesizers, they also remove carbon dioxide from the atmosphere. Phytoplankton that elude predation sink to the bottom of the ocean when they die, taking atmospheric carbon with them where it will remain for centuries [2]. This process is known as the biological pump. The biological pump plays a crucial role in the Earth’s carbon cycle and is greatly influenced by seasonal phytoplankton blooms [3, 4, 5]. Research has been conducted concerning the utility of triggering blooms by fertilizing parts of the ocean with nutrients as a method of combating climate change [6]. In order to understand the relative magnitude of the biological pump, understanding the dynamics of the plankton system in the surface ocean is critical.

1.2 The Phenomenon of Blooms

Many regions of the world’s oceans experience a seasonal phenomenon known as a plankton bloom, which is a significant increase in phytoplankton population [7]. The precise threshold definition of these blooms has been debated [8, 9, 10, 11]. For our purposes, we will use the word “bloom” to represent the rapid onset of phytoplankton biomass. Like plants, phytoplankton require sunlight and nutrients to live, grow and reproduce. Photosynthesis in the ocean can only occur in an upper layer known as the “euphotic zone” or “photic zone” [1]. The availability of nutrients is dependent on biological and physical processes in the ocean. In order for a bloom to occur,
phytoplankton must have access to ample nutrients and sunlight, have sufficiently low pressure from predators, namely zooplankton, and they cannot sink out of the euphotic zone too quickly.

Access to sunlight for phytoplankton depends on how deep the phytoplankton are, and how turbid the water is. The intensity of sunlight in the ocean decays with increasing depth [1]. The euphotic zone is defined to extend from the surface to a depth at which the sunlight intensity is one percent of that at the surface, known as the euphotic depth, below which photosynthesis essentially cannot occur [12]. The sunlight intensity at the surface depends on the latitude of the region in question and the time of the year. At any latitude, the annual surface sunlight intensity reaches its maximum at the summer solstice and reaches its minimum at the winter solstice. However, surface sunlight intensity always decreases with distance from the equator due to the lower angle of the sun [1].

Access to nutrients for phytoplankton can be facilitated by a variety of factors. Nutrients can be deposited in the ocean by runoff from rivers, upwelling in the ocean, and fecal pellets from birds and aquatic animals. Dead phytoplankton and zooplankton remineralize (decompose) into chemical forms that can serve as a nutrient source for phytoplankton. Hence, phytoplankton obtain some of their food from remineralized plankton.

The upper mixed layer of the ocean is known to influence the availability of sunlight and nutrients for phytoplankton. Near the surface, the ocean is subject to several sources of turbulence such as wind, breaking surface and internal waves, and Langmuir circulation [13]. In wintertime, turbulence is also created by colder, denser water sinking beneath the warmer, less dense water below [14]. All of this turbulence causes mixing in a layer at the surface of the ocean known as the mixed layer. The thickness of the mixed layer, and consequently the mixed layer depth (MLD), varies seasonally. Winter months are colder and have more storms than do summer months and hence, the MLD is deeper in the winter than in the summer [15]. The deepening of the mixed layer depth mixes water from the lower ocean with surface water, producing
an upwelling of deep nutrients [16]. This helps to supply phytoplankton with nutrients but a deep mixed layer can periodically pull phytoplankton down, limiting their time in the euphotic zone. On the other hand, the shoaling of the mixed layer depth prevents phytoplankton from being pulled too deep, keeping them in or near the euphotic zone. This gives them more access to sunlight.

1.3 Plankton Bloom Models and Theory

The cause of blooms has been debated for decades. In 1953, H. U. Sverdrup published what became the canonical theory known as the Critical Depth Hypothesis [11]. Sverdrup states that in order for a bloom to begin, the production of organic matter by photosynthesis in the mixed layer must exceed the destruction of organic matter by respiration. A schematic of Sverdrup’s model is given in Figure 1.1 (redrawn from [17]). The rates of phytoplankton production and phytoplankton respiration are plotted against depth. The destruction of organic matter happens continuously wherever there are plants or animals. Hence, it is assumed that phytoplankton respiration is constant with depth as shown on the graph. Since sunlight intensity attenuates exponentially with depth then phytoplankton production is represented by a function that decays exponentially with depth on the graph. The total production in the mixed layer is the integral under the “production curve” (i.e. the area of the shape “a-b-c-d”). The total phytoplankton respiration in the mixed layer is the integral under the “respiration curve” (i.e. the area of the rectangle “a-e-f-d”). The compensation depth, $D_C$, is the depth at which the rate of production is equal to the rate of respiration. When the mixed layer depth is at or above the compensation depth, the total production is greater than the total phytoplankton respiration. However, the total production can sometimes exceed the total phytoplankton respiration when the mixed layer depth is below the compensation depth. The depth at which the total production equals the total phytoplankton respiration ($\text{Area}(a-b-c-d) = \text{Area}(a-e-f-d)$) is called the “critical depth.” Theoretically, blooms may happen when the mixed layer depth is above the critical depth but not below. According to Sverdrup, the spring shoaling of the mixed
layer depth initiates a bloom when the mixed layer depth becomes shallower than the critical depth.

Although the Critical Depth Hypothesis is widely cited, the theory has its limitations. Sverdrup’s model was based on simplifying assumptions. Here, three of them are discussed.

1. Within the mixed layer the turbulence is strong enough to distribute the plankton evenly throughout the layer.
2. Nutrients are always in abundance in the mixed layer.
3. Respiration is constant with depth.

The first assumption is closer to reality in high latitudes than it is in lower latitudes. High latitude oceanic regions have stronger and more frequent winter storms than their low latitude counterparts. Therefore, high latitude regions are more likely to have a well-mixed upper layer that distributes plankton evenly. The second assumption is
not always true in the ocean. Several factors can cause the nutrient concentration to increase. For instance, a deepening mixed layer can upwell nutrients from the lower ocean. Sandstorms can blow a large amount of minerals into the ocean. Hurricanes can bring nutrients to the surface, often leaving phytoplankton blooms in their wake. An oceanic region can also become nutrient poor when a bloom becomes too large; there is no longer a sufficient concentration of nutrients to sustain the bloom. The third assumption allows the Critical Depth Hypothesis to work in theory. Respiration that is constant with depth facilitates the geometric definition of critical depth outlined at the beginning of this section. However, it is a bold assumption that has been challenged [8]. The Critical Depth Hypothesis has also been criticized for its inability to explain observations of phytoplankton growth prior to mixed layer shoaling [8, 18, 19].

Sverdrup also had limited data to support his theory. His data was collected in the spring of 1949 onboard Weather Ship “M” stationed in the Norwegian Sea (66°N, 2°E). Modern oceanographers have access to satellite data from almost every region in the world’s oceans.

In 2010, Michael Behrenfeld published a paper that directly challenged Sverdrup’s Critical Depth Hypothesis [8]. Having the benefit of satellite data, Behrenfeld studied several “pseudo-rectangular” regions in the North Atlantic. Each of these regions spans five degrees of latitude and ten degrees of longitude. He observed four quantities: phytoplankton carbon concentration ($C_{phyt}$), chlorophyll concentration ($Chl_{sat}$), mixed layer depth (MLD), and photosynthetically active radiation (PAR). Photosynthetically active radiation is solar energy that can be used for photosynthesis, which is light in the 400 to 700 nm wavelength range [20]. Figure 1.2 shows a time series of these four quantities averaged over the North Atlantic region within 45-50°N and 25-35°W from 1998 through 2006. The rapid increase of either $C_{phyt}$ (black) or $Chl_{sat}$ (green) indicates when the phytoplankton are in bloom. Behrenfeld makes the critical observation that the blooms initiate when the mixed layer depth is still deepening. This is only possible if respiration is not constant in time or depth, contradicting Sverdrup’s assumption. This at least proves that blooms are not always initiated by the shoaling
Figure 1.2: Satellite time series of phytoplankton carbon concentration ($C_{phyt}$: black), chlorophyll concentration ($Chl_{sat}$: green), photosynthetically active radiation (PAR: red), and mixed layer depth (MLD: blue) averaged over the North Atlantic region within 45-50°N and 25-35°W from 1998 through 2006 [8]. Used with permission: see appendix D.

Behrenfeld proposed to replace the critical depth hypothesis with his “Dilution-Recoupling Hypothesis.” He posits that the deepening of the mixed layer, which upwells water from the lower ocean, dilutes the plankton in the upper ocean. This has the effect of predator-prey decoupling (i.e. physically separating phytoplankton from zooplankton). With grazing pressure from the zooplankton reduced, the phytoplankton bloom. The cessation of mixed layer deepening causes predator-prey recoupling, which eventually ends the bloom.

Alternatively, there is also the Critical Turbulence Hypothesis, which states that there is a critical level of turbulence (indicated by a turbulent diffusivity parameter) below which blooms can occur regardless of the mixed layer depth. This theory reconceptualizes the upper mixed layer as the turbulent surface layer. According to
this theory, phytoplankton can bloom when the growth rate is higher than the vertical mixing rate. This challenges the assumption from the Critical Depth Hypothesis that mixing is constant in the surface layer. However, the Critical Depth Hypothesis and the Critical Turbulence Hypothesis are similar. Just as the Critical Depth Hypothesis says there should be no bloom with deep mixing because it reduces the growth rate, the Critical Turbulence Hypothesis says blooms cannot form when turbulent mixing is higher than the growth rate. For details we direct the reader to Huisman et al. [10], Chiswell [21], Brody and Lozier [22], and Ferrari et al. [23].

Each of these theories has been invoked to explain observed patterns in plankton observations. For example, Nelson and Smith [24] invoke the Critical Depth Hypothesis to ice-edge phytoplankton blooms in the Southern Ocean. Some studies deviate only slightly from the original Critical Depth Hypothesis [25, 26]. Taylor and Ferrari [14] invoke the Critical Turbulence Hypothesis as a foundation for their theory of spring phytoplankton blooms in the North Atlantic triggered by the spring shutdown of turbulent convection. Smith et al. [27] invoke the Dilution-Recoupling Hypothesis to explain North Atlantic phytoplankton blooms. Behrenfeld et al. [28] expand on the Dilution-Recoupling Hypothesis by recognizing that the decoupling of plankton dynamics through dilution is one of many processes that contribute to phytoplankton blooms. Fischer et al. [9] highlight major theories of phytoplankton blooms since Sverdrup’s study was published. However, ad-hoc explanations that describe the temporal pattern in plankton populations may overlook important dynamical structures of the underlying plankton ecosystem. These structures will be discussed in this dissertation.

1.4 Mathematical Challenges

Modeling phytoplankton blooms presents many mathematical challenges. To start, there are thousands of known species of plankton, each with its own unique growth and feeding behavior. Quantities such as phytoplankton growth rates, nutrient uptake rates by phytoplankton, zooplankton grazing rates on phytoplankton and the like have been estimated for certain species isolated in laboratory experiments. But
no one species of phytoplankton or zooplankton is isolated in the ocean. If one wishes to model the behavior of plankton at a specific location then they must either limit the number of plankton species in their model or estimate the overall behavior of the plankton as a group.

Plankton and nutrients are also subject to a multitude of physical processes that cause transport of ocean water in every direction. At any specific location, it is impossible to determine all of the physical forces acting on the plankton. If one wishes to model the movement of plankton then he/she must determine the dominant force(s) acting on the plankton based on the location being studied and the available data. As mentioned before, the ocean’s mixed layer is subject to turbulence. Turbulent diffusivity in the ocean is difficult to measure and is subject to estimation.

Comparing a plankton ecology model to data is also a challenge. Estimation of the phytoplankton biomass in an ocean locality can be done with satellites. The above mentioned $C_{phyt}$ and $Chl_{sat}$ quantities are useful for this purpose. However, satellites can only see as far down in the ocean as the turbidity will allow. Therefore, satellites can only observe concentrations of phytoplankton at or near the surface of the ocean. Also, only in situ observations are practical for estimating local quantities of nutrients and zooplankton. But again, due to the vastness and depth of the ocean, in situ measurements are made at too small of a scale to estimate the amount of nutrients and zooplankton in an area large enough to be covered by a phytoplankton bloom. So when modeling on the scale of a phytoplankton bloom, while phytoplankton biomass can be compared with data, the same cannot be accomplished with zooplankton or nutrients.

1.5 A New Approach

Nutrient-Phytoplankton-Zooplankton (NPZ) models have been used to study marine plankton ecology, seasonal phytoplankton blooms, and spatial plankton distribution among other natural processes [29, 30, 31, 32, 33, 34, 35, 36, 37]. However, the biological and physical processes that affect plankton communities are so numerous that
no NPZ model can account for all of them explicitly and accurately. Many studies involving mathematical plankton models attempt to simulate additional biogeochemical processes by adding more state variables such as multiple species/groups of phytoplankton and/or zooplankton [38, 39, 40, 41, 42, 43, 44, 45, 46] to accommodate for diversity in a plankton community. Some add a state variable for detritus ($D$) which simulates organic matter lost from plankton that must remineralize into nutrients ($N$) before it can be taken up again by phytoplankton. This introduces yet another parameter for the detritus remineralization rate, which makes it more difficult to understand the behavior of the model. Many such studies produce results that successfully mimic natural marine phenomena such as seasonal phytoplankton blooms, species composition of plankton communities in specific oceanic regions, and spatial plankton distribution through techniques such as parameter optimization [47, 48, 49, 35, 50, 51]. However, interpreting the significance of the parameters from these complex models often comes from examining how well the simulated results match in-situ records. Understanding the underlying dynamics of a model may bring more insight into its behavior, and into the ecological principles governing plankton communities [52, 53].

Appropriate construction of an NPZ model depends on the nature and complexity of the process of interest. A system of coupled ordinary differential equations usually suffices for an NPZ model constructed for simulating biological processes without spatially dependent physical forcing. Busenberg et al. [52] analyzed the dynamics of a simple, autonomous NPZ model composed of ordinary differential equations, giving insight into spatially independent marine plankton ecology. Their model and dynamical study has been used as a foundation for more complex models [40, 53]. However, the ocean subjects plankton communities to physical forcing from solar radiation and from depth-dependent turbulent mixing, effects which are missing from this model.

Behrenfeld and Boss [54] argue that a paradigm shift is needed as to the way blooms are explained. They suggest that changes in mixed layer depth and sunlight disrupt the balance of the phytoplankton-zooplankton equilibria. In other words, phytoplankton bloom formation or termination represents a transition from one ecological
state to another as light and mixed layer depth change. This is the approach examined in this dissertation.

We consider a Nutrient-Phytoplankton-Zooplankton (NPZ) model, a system of coupled, nonlinear partial differential equations, to simulate phytoplankton blooms. Since the quantities of solar radiation intensity, mixed layer thickness, and turbulent diffusivity have been used to understand theoretical causes of phytoplankton blooms, these quantities are incorporated into the model. An autonomous form of an NPZ model (with no time dependence in its coefficients) can have multiple equilibrium states. The state of such a system depends on the values of the model coefficients. Time dependent coefficients can cause the attracting equilibrium state of the system to periodically change from one state to another. Thus, the values of the state variables \( N, P, \) and \( Z \) depend on which equilibrium state is attracting. However, whether the model simulates a phytoplankton bloom or not also depends on the state of the system (current values for \( N, P, \) and \( Z \)).

We begin our explanation of the bloom process with an NPZ model that is a system of three coupled ordinary differential equations (one for each state variable \( N, P, \) and \( Z \)) with a time-dependent coefficient that imitates seasonally oscillating solar radiation. Without time dependence, the resulting autonomous model has three equilibrium states determined by Busenberg et al. [52]: plankton free, phytoplankton only, and co-existing phytoplankton and zooplankton. Busenberg et al. [52] also show that only one of these states can be attracting while the other two must repel. In the ordinary differential equations model of this dissertation, which includes a time-dependent coefficient that imitates seasonally oscillating solar radiation, it is determined analytically which equilibrium state the system is in and how the system changes from one attracting state to another. Analysis of the dynamics of the autonomous ordinary differential equations model provides information that explains similar behavior in an NPZ model with seasonal solar forcing and inclusion of mixed layer depth and diffusion.

To obtain a model that simulates blooms that reflect actual phytoplankton blooms in the ocean, we incorporate diffusion (used as a proxy for turbulent mixing)
and mixed layer depth into the ordinary differential equations model, resulting in a reaction-diffusion system. Incorporating these two quantities allows for an evaluation of the uses of these quantities in existing bloom theories. The Critical Depth Hypothesis and the Dilution-Recoupling Hypothesis attribute phytoplankton blooms to the seasonal changes in mixed layer depth whereas the Critical Turbulence Hypothesis attributes phytoplankton blooms to changes in levels of turbulent mixing. We find that these quantities have effects on the blooming behavior of our model that somewhat agree with these theories. However, our analysis suggests that mixed layer depth and diffusion, along with solar radiation, drive phytoplankton blooms primarily by affecting which equilibrium of our model is attracting. Using the techniques of Edwards et al. [53], the equilibrium states of the reaction-diffusion model and the conditions under which they attract are determined computationally. The effect of seasonal data on the dynamics of the NPZ reaction-diffusion system is analyzed graphically, allowing interpretation of how seasonal data determines which of the three equilibrium states is attracting. Analysis of the ordinary differential equations model illuminates the process of a phytoplankton bloom in the reaction-diffusion model. This analysis suggests a mechanism for the cause of marine phytoplankton blooms that agrees with Behrenfeld and Boss’ theory that blooms result from disruptions in predator-prey equilibria [54].

1.6 Outline of Dissertation

This dissertation is organized as follows. In chapter 2, as in Cowall et al. [55], an ordinary differential equations model is constructed by incorporating a light response coefficient into the model of Franks, Wroblewski, and Flierl [56]. The effect of changing the value of this coefficient on the dynamics of the system is examined, with attention to conditions that facilitate a model phytoplankton bloom. Then, a sinusoidal function is used for the light input to drive the system. Blooms in this model initiate immediately after the oscillating light response coefficient passes its minimum value. This effect is analogous to a phytoplankton bloom initiating immediately after the winter solstice, which is far earlier than blooms begin in the North Atlantic Ocean.
Therefore, in chapter 3, the model is enhanced to a reaction diffusion system that incorporates spatial effects such as diffusion, mixed layer depth, and attenuation of light with depth. We linearize this system and compute the equilibria. The results of the dynamical analysis are presented with respect to light, diffusion, and mixed layer depth. The techniques of Edwards et al. [53] are used to render stability diagrams like those from Cowall et al. [55] to inform our choice of parameters and to help determine the necessary conditions to cause a bloom in the reaction-diffusion system. In chapter 4, solar radiation and mixed layer depth data from the North Atlantic Ocean are incorporated into the reaction-diffusion model. The resulting phytoplankton predictions are compared to North Atlantic chlorophyll data. The improvements of bloom timing resulting from the incorporation of diffusion, mixed layer depth, and attenuation of light with depth are discussed. Limitations of the reaction-diffusion model are also discussed. Finally, similarities between the results of this dissertation and others are discussed that suggest the presence of a saddle point bloom mechanism (SPM).
2.1 NPZ Models

2.1.1 Principles of NPZ Models

In this chapter, a plankton ecology model is constructed to study phytoplankton blooms in the ocean. The model of choice is a form of an NPZ (Nutrient-Phytoplankton-Zooplankton) model. It is a system of coupled, time-dependent differential equations with three state variables: nutrients ($N$), phytoplankton ($P$), and zooplankton ($Z$). Assuming that nitrogen is the limiting nutrient of the ecosystem, we use millimoles of nitrogen per meter cubed (mmol N m$^{-3}$) as the unit of the nutrient variable. Technically, the variable $P$ represents the concentration of nitrogen in phytoplankton and the variable $Z$ represents the concentration of nitrogen in zooplankton. Thus, nitrogen is interpreted as the “currency” of the model. This way, we can use mmol N m$^{-3}$ as the unit for each state variable. For brevity, we shall henceforth refer to the $P$ and $Z$ variables as the concentrations of phytoplankton and zooplankton, respectively.

2.1.2 Structure of NPZ Models

To construct an NPZ model, one must choose “transfer” functions to describe the transfer of nitrogen from one state variable to another. Figure 2.1 shows a schematic that outlines the biological processes of the plankton community being modeled. The transfer functions are symbolized by the arrows between the state variables. $g(N)$ describes the rate of nutrient uptake by phytoplankton. $h(P)$ describes the rate of
Figure 2.1: Schematic of an NPZ model. State variables: nutrients \((N)\), phytoplankton \((P)\), and zooplankton \((Z)\). “Transfer functions”: phytoplankton uptake of nutrients \(g(N)\), zooplankton grazing on phytoplankton \(h(P)\), mortality rate of phytoplankton \(m_P(P)\), and mortality rate of zooplankton \(m_Z(Z)\).

zooplankton grazing on phytoplankton. \(m_P(P)\) and \(m_Z(Z)\) describe the mortality rates of phytoplankton and zooplankton, respectively.

Equation (2.1) utilizes the structure of the schematic in figure 2.1 in the form of three coupled, ordinary differential equations. The equation incorporates a function describing the phytoplankton’s response to sunlight, \(f(I)\), where \(I\) is irradiance (sunlight), according to Franks [32]. The rate of change in the concentration of nutrients, phytoplankton, and zooplankton are represented by \(\frac{dN}{dt}\), \(\frac{dP}{dt}\), and \(\frac{dZ}{dt}\), respectively.

\[
\begin{align*}
\frac{dP}{dt} &= f(I)g(N)P - h(P)Z - m_P(P)P \\
\frac{dZ}{dt} &= \alpha h(P)Z - m_Z(Z)Z \\
\frac{dN}{dt} &= -f(I)g(N)P + (1-\alpha)h(P)Z + m_P(P)P + m_Z(Z)Z
\end{align*}
\]

An increase in the phytoplankton growth term \((f(I)g(N)P \geq 0)\) (i.e. phytoplankton have access to more sunlight \(I\) and more nutrients \(N)\) contributes to an
increase in phytoplankton concentration. An increase in the grazing rate \( h(P) \) or phytoplankton mortality rate \( m_P(P) \) contributes to a decrease in phytoplankton concentration. The uptake of nutrients by phytoplankton contributes to a decrease in the concentration of nutrients and thus the phytoplankton growth term \( f(I)g(N)P \) reappears with a negative sign in the nutrient equation. An increase in the grazing rate contributes to an increase in the zooplankton concentration and thus the grazing term \( h(P)Z \) reappears in the zooplankton equation. However, it takes more than one prey consumed to produce another predator. Therefore the zooplankton growth term includes the coefficient \( \alpha \), where \( 0 < \alpha < 1 \). An increase in the zooplankton mortality rate \( m_Z(Z) \) contributes to a decrease in the zooplankton concentration. As noted in section 1.2, dead plankton can be remineralized into food for phytoplankton. Thus the mortality terms for phytoplankton \( m_P(P) \) and zooplankton \( m_Z(Z) \) reappear with positive signs in the nutrient equation. In the nutrient equation, the term \((1-\alpha)h(P)Z\) represents the portion of biomass consumed by zooplankton that is excreted and becomes nutrients.

An NPZ model of this structure works under certain assumptions.

1. The concentrations of the quantities \( N, P, \) and \( Z \) are completely controlled by the processes of photosynthesis, nutrient uptake, grazing, mortality, excretion, and remineralization.

2. All zooplankton excretions and dead plankton are recycled into nutrients.

3. The system is closed; the total amount of nitrogen is constant as \( \frac{dN}{dt} + \frac{dP}{dt} + \frac{dZ}{dt} = 0 \). Thus, there are no sources or sinks of nutrients.

Other factors affecting the ecosystem, such as sea temperature, are neglected. As indicated in chapter 1, there are several sources and sinks of nutrients in the ocean. We also neglect the portion of the dead plankton that sink to the bottom of the ocean.

The third assumption implies that the total nitrogen in the system is conserved. This allows the introduction of the constant \( N_T = N + P + Z \), the total concentration of nitrogen in the system. This allows us to write \( N = N_T - P - Z \) and reduce the system to two equations as is done in section 2.2.
2.2 Constructing an Ordinary Differential Equations NPZ Model

We begin with the construction of a basic ordinary differential equation model.

\[ \frac{dP}{dt} = \rho \mu_{max} \frac{N}{k_N + N} P - h_{max} \left(1 - e^{-aP}\right) Z - m_P P \]

\[ \frac{dZ}{dt} = \alpha h_{max} \left(1 - e^{-aP}\right) Z - m_Z Z \]

\[ \frac{dN}{dt} = -\rho \mu_{max} \frac{N}{k_N + N} P + (1 - \alpha) h_{max} \left(1 - e^{-aP}\right) Z + m_P P + m_Z Z \]

This model is inspired by Franks et al. [56], but here we add a light response, \( \rho = \rho(I) \) where \( I = I(t) \) is the intensity of the solar radiation at the surface and \( 0 < \rho \leq 1 \). Note that the system (2.2) is equivalent to the model of Franks et al. [56] if \( \rho \equiv 1 \). The nutrient uptake rate of phytoplankton is described by the Michaelis-Menten function \( g(N) = \mu_{max} \frac{N}{k_N + N} \) [57]. The parameter \( \alpha \) is the zooplankton’s assimilation efficiency of phytoplankton. The grazing rate of phytoplankton by zooplankton is represented by the Ivlev function \( h(P) = h_{max} \left(1 - e^{-aP}\right) \) [58]. NPZ models with other common grazing functions have been analyzed [59, 60, 61, 62, 63, 64, 65, 66] but we choose the Ivlev function so that we can build from the detailed analysis of Busenberg et al. [52]. Although NPZ models with different grazing functions exhibit a diversity of behavior, blooming behavior of NPZ models with the Ivlev grazing function are similar to that of NPZ models with other grazing functions. Table 2.1 gives a description of the parameters and our chosen values for them. By design, the right-hand side of the system sums to zero so that the total concentration of nitrogen in the system is conserved. Therefore, we can write \( N + P + Z = N_T \), where the constant \( N_T \) is the total concentration of nitrogen in the system. Thus, we can reduce system (2.2) to the two equations (2.3).

\[ \frac{dP}{dt} = \rho \mu_{max} \frac{N_T - P - Z}{k_N + N_T - P - Z} P - h_{max} \left(1 - e^{-aP}\right) Z - m_P P \]

\[ \frac{dZ}{dt} = \alpha h_{max} \left(1 - e^{-aP}\right) Z - m_Z Z \]
Table 2.1: Parameter descriptions and values for equations (2.2). Values from Gentleman and Neuheimer [61].

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>α</td>
<td>Assimilation efficiency</td>
<td>0.7</td>
<td>-</td>
</tr>
<tr>
<td>$\mu_{max}$</td>
<td>Phytoplankton maximum growth rate</td>
<td>2</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>a</td>
<td>Ivlev decay constant</td>
<td>1</td>
<td>(mmol N m$^{-3}$)$^{-1}$</td>
</tr>
<tr>
<td>$h_{max}$</td>
<td>Maximum grazing rate</td>
<td>1.5</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$k_N$</td>
<td>Michaelis-Menten half-saturation constant</td>
<td>1</td>
<td>mmol N m$^{-3}$</td>
</tr>
<tr>
<td>$m_P$</td>
<td>Phytoplankton mortality rate</td>
<td>0.1</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$m_Z$</td>
<td>Zooplankton mortality rate</td>
<td>0.2</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$N_T$</td>
<td>Total nitrogen in the system</td>
<td>2</td>
<td>mmol N m$^{-3}$</td>
</tr>
</tbody>
</table>

2.3 Dynamics of the Ordinary Differential Equations NPZ Model

A stability analysis of the coupled equations (2.3) with the parameter $\rho \equiv 1$ was carried out by Busenberg et al. [52]. In their paper, there are three equilibria. The equivalent equilibria when the parameter $\rho$ is included are:

- a “plankton-free” equilibrium $(P, Z, N) = (0, 0, N_T)$,
- a “phytoplankton-only” equilibrium $(P, Z, N) = (\bar{P}, 0, N_T - \bar{P})$,
- a “coexisting” equilibrium $(P, Z, N) = (P^*, Z^*, N_T - P^* - Z^*)$,

where

$$\bar{P} = N_T - \frac{m_P k_N}{\rho \mu_{max} - m_P} > 0, \quad P^* = -\frac{1}{a} \ln \left(1 - \frac{m_Z}{\alpha h_{max}}\right) > 0,$$

and $Z^*$ being the unique solution satisfying $0 < Z^* < N_T - P^*$ of the quadratic equation

$$Z^2 - Z \left[\frac{\alpha (\rho \mu_{max} - m_P) P^*}{m_Z} + k_N + N_T - P^*\right] + P^* \frac{\alpha}{m_Z} [(\rho \mu_{max} - m_P)(N_T - P^*) - k_N m_P] = 0.$$
Busenberg et al. [52] defined the following additional parameters. As noted previously, their analysis did not include the parameter $\rho$; here we have extended their analysis to include it, thus setting $\rho \equiv 1$ recovers their results.

$$R_0 = \frac{\rho \mu_{max} N_T}{m_P (k_N + N_T)}$$  \hspace{1cm} (2.6)

$$R_1 = \frac{\alpha h_{max} (1 - e^{-\alpha P})}{m_Z}$$  \hspace{1cm} (2.7)

$$R_2 = \frac{\rho \mu_{max} - m_P}{\alpha h_{max} Z^* (1 - \frac{m_Z}{\alpha h_{max}}) + \frac{\rho k N_{max} (k_N + N_T - Z^*)}{(k_N + N_T - Z^* - P^*)^2}}$$  \hspace{1cm} (2.8)

These additional parameters determine the existence and stability of the equilibria according to the following conditions [52].

1. The equilibrium $(P, Z, N) = (0, 0, N_T)$ always exists and is stable if and only if $R_0 < 1$.

2. If $R_0 > 1$ then the equilibrium $(\bar{P}, 0, N_T - \bar{P})$ exists and is stable if and only if $R_0 > 1$ and $R_1 < 1$.

3. If $R_1 > 1$ then the equilibrium $(P^*, Z^*, N_T - P^* - Z^*)$ exists and is stable if and only if $R_0 > 1$, $R_1 > 1$, and $R_2 < 1$.

4. If $R_2 > 1$ then $(P^*, Z^*, N_T - P^* - Z^*)$ is unstable but is surrounded by at least one closed orbit indicating a periodic solution.

To investigate the dependence on the parameter $\rho$, which depends on the available sunlight, we change the parameter $\rho$ while holding the other model parameters constant. This changes which of the above stability conditions hold. We define the parameter

$$\bar{P}_E = \frac{m_P (k_N + N_T)}{\mu_{max} N_T}$$  \hspace{1cm} (2.9)

such that the phytoplankton-only equilibrium exists if $\rho > \bar{P}_E$ and we define

$$\bar{P}_S = \frac{m_P}{\mu_{max}} \left[ 1 + \frac{k_N}{N_T - \frac{1}{a} \ln \left( \frac{\alpha h_{max}}{\alpha h_{max} - m_Z} \right)} \right]$$  \hspace{1cm} (2.10)
such that the phytoplankton-only equilibrium is stable if $\rho < \bar{P}_S$. Then from (2.6), (2.7), and the second stability condition, we have existence and stability of the phytoplankton-only equilibrium when $\bar{P}_E < \rho < \bar{P}_S$. From (2.10), we see that $\bar{P}_S$ increases with $m_Z$ and decreases with $h_{\text{max}}$ and $a$. Thus, increasing $m_Z$ or decreasing $h_{\text{max}}$ or $a$ causes the interval $(\bar{P}_E, \bar{P}_S)$ to widen, which increases the range of $\rho$ for which the phytoplankton-only equilibrium is stable. When $\rho > \bar{P}_S$, the coexisting equilibrium is stable if $R_2 < 1$. With the parameter values from Table 2.1 we have $\bar{P}_E = 0.075$ and $\bar{P}_S = 0.078$. Note that $R_2$ is not a monotonic function of $\rho$; see Figure 2.2. There is no upper bound for $\rho$ for which $R_2 < 1$. Figure 2.3 shows phase planes of the solution of (2.3) where the plankton-free equilibrium is stable ($\rho < \bar{P}_E$), where the phytoplankton-only equilibrium is stable ($\bar{P}_E < \rho < \bar{P}_S$), where the coexisting equilibrium is stable ($\rho > \bar{P}_S$ and $R_2 < 1$), and where the coexisting equilibrium is unstable and repels nearby trajectories toward a closed orbit ($R_2 > 1$).

Using the thresholds $\bar{P}_E$ and $\bar{P}_S$, we can rewrite the first three stability conditions.

1. The equilibrium $(P, Z, N) = (0, 0, N_T)$ always exists and is stable if and only if $\rho < \bar{P}_E$.

2. If $\rho > \bar{P}_E$ then the equilibrium $(\bar{P}, 0, N_T - \bar{P})$ exists and is stable if and only if $\bar{P}_E < \rho < \bar{P}_S$.

3. If $\rho > \bar{P}_S$ then the equilibrium $(P^*, Z^*, N_T - P^* - Z^*)$ exists and is stable if and only if $\rho > \bar{P}_S$, and $R_2 < 1$.

These properties aid in understanding why certain behaviors of the parameter $\rho$ yield a phytoplankton bloom from the system (2.3). To get a complete picture of the mechanisms that cause a model bloom, one needs to keep in mind two results from Busenberg et al. [52]. First, $\bar{P} > P^*$ whenever $P^*$ exists. Second, it follows from Busenberg et al. [52] that when $\rho > \bar{P}_S$, the phytoplankton-only equilibrium is a saddle point with stable manifold $\{(P, Z) : Z = 0, 0 < P \leq N_T\}$, the horizontal axis. Figure 2.4 illustrates an example of a saddle point.
Figure 2.2: $R_2$ as a Function of $\rho$. Only values of $\rho$ where $\rho > \bar{P}_S$ are considered since the coexisting equilibrium does not exist where $\rho < \bar{P}_S$. Embedded graph shows that $R_2 < 1$ when $\rho$ is close to 1. Parameter values from Table 2.1.
Figure 2.3: Phase plane trajectories of solutions of equations (2.3) illustrating the three types of equilibria with parameter values from Table 2.1. In each case, the trajectory starts at the circle. The stable equilibrium is marked by an ‘×’ except in (d) where ‘×’ is an unstable coexisting equilibrium. In (a), $\rho = 0.07$, implying $\rho < \bar{P}_E$ which means the plankton-free equilibrium is the only equilibrium and stable. In (b), $\rho = 0.076$, implying $\bar{P}_E < \rho < \bar{P}_S$ which means the phytoplankton-only equilibrium is the only attractor. In (c) $\rho = 0.09$, implying $\rho > \bar{P}_S$ and, from Figure 2.2, $R_2 < 1$. This means that the coexisting equilibrium the only attractor. In (d) $\rho = 0.3$ which, from Figure 2.2, means $R_2 > 1$, indicating that all equilibria are unstable. A closed orbit surrounds the unstable coexisting equilibrium.
Figure 2.4: The equilibrium in this illustration, the red “x,” is a saddle point. Trajectories that start close to the stable manifold (blue line) will pass by the equilibrium and then move away from it asymptotically along the unstable manifold (green line).

2.4 Saddle Point Bloom Mechanism in an Ordinary Differential Equations NPZ Model

To illustrate the saddle point bloom mechanism, equations (2.3) are solved using artificial values for \( \rho(t) \). For now, \( \rho \) is expressed as a function of \( t \), not as a function of \( I \), because data is not used in this illustrative example. A function \( \rho(I) \) will be defined later and solar radiation data will then be used for \( I(t) \). As a simple example, assume a year has 360 days with day 1 being the summer solstice. This way, it is easy to remember that day 90 is the autumnal equinox, day 180 is the winter solstice, and day 270 is the vernal equinox. For now, the substitution for \( \rho \) is

\[
\rho(I(t)) \equiv \rho(t) = 0.45 \cos \left( \frac{2\pi}{360} t \right) + 0.55. \tag{2.11}
\]

This approximation has a maximum of 1, a minimum of 0.1, and a period of 360 days. Initial conditions are set to \((P,Z,N) = (0.2,0.2,1.6)\) as chosen by Gentleman and
Neuheimer [61]. Figure 2.5 shows this result starting after 360 days, when the solution becomes periodic. For brevity, we shall refer to this solution as the “non-autonomous solution” since $\rho$ depends on $t$.

In the top plot of Figure 2.5, the minimum of $\rho$ is slightly larger than $\bar{P}_S$, which is 0.0934. Consequently, for the duration of this time series, the coexisting equilibrium exists (Condition 3) and the phytoplankton-only equilibrium is a saddle point. In the bottom plot of Figure 2.5, the phytoplankton concentration reaches its annual minimum at approximately the winter solstice (day 180) and the zooplankton concentration reaches its annual minimum about 20 days later. After the winter solstice, the phytoplankton bloom under increasing sunlight and reduced grazing pressure from zooplankton. This bloom lasts up to approximately the vernal equinox (day 270) and declines with the growth of zooplankton.

The mechanics of the saddle point bloom mechanism in Figure 2.5 is illustrated
with phase planes. The phase planes in Figure 2.6 show fifty-day solution trajectories of system (2.3) at three different sets of initial conditions with light response $\rho$ held constant (which makes system (2.3) autonomous). The initial conditions for each figure are selected as the values $P$ and $Z$ on a different day from the non-autonomous solution (bottom plot of Figure 2.5). To envision the trajectory’s path as the seasons change, the value of $\rho$ in each figure is set to the value 50 days in the future, allowing for the visualization of the saddle point bloom mechanism. Each trajectory spirals toward the coexisting equilibrium and is also influenced by the phytoplankton-only equilibrium, which is a saddle point. When zooplankton are low, the saddle point temporarily attracts along the stable manifold ($Z = 0$) and then repels along the unstable manifold (Figure 2.6, dashed line). The slope of the unstable manifold depends on $\rho$. In Figure 2.6a, the initial conditions are set to the values of $P$ and $Z$ on day 80 of the non-autonomous solution (see Figure 2.5) and the light response coefficient $\rho$ is set to the value of $\rho(t)$, from (2.11), on day 130. The trajectory spirals toward the coexisting equilibrium of the system (2.3) (marked by a red $\times$) that has a significantly lower concentration of zooplankton than the initial conditions. The terminal point of the fifty-day trajectory (marked by a magenta asterisk) falls close to the coexisting equilibrium. Figure 2.6b shows the autonomous solution with initial conditions set to the values of $P$ and $Z$ on day 130 of the non-autonomous solution, and the value of $\rho$ corresponding to day 180 (the winter solstice) of $\rho(t)$ from (2.11). Again, the trajectory spirals toward the coexisting equilibrium. However, the terminal point of the fifty-day trajectory falls well short of the coexisting equilibrium for reasons to be discussed shortly. Figure 2.6c shows the autonomous solution with initial conditions corresponding to day 180 of the non-autonomous solution and $\rho$ corresponding to day 230 of $\rho(t)$ from (2.11). This time, the fifty-day trajectory moves horizontally towards the phytoplankton-only equilibrium (marked by a green “plus” sign +) and then turns towards the coexisting equilibrium, terminating close to it. This behavior is expected because the phytoplankton-only equilibrium is a saddle point with stable manifold $\{(P, Z) : Z = 0, 0 < P \leq N_T\}$ whenever the coexisting equilibrium exists, as shown by
Busenberg et al. [52]. These results indicate that light determines how much influence
the saddle point has on the trajectory of the system.

It is important to observe that \( \bar{P} \) increases with increasing \( \rho \) whereas \( P^* \) does not
depend on \( \rho \), see equation (2.4). In the coexisting equilibrium \((P^*, Z^*)\), only the zoo-
plankton value \( Z^* \) depends on \( \rho \); see equation (2.5). Consequently, the phytoplankton-
only equilibrium (green plus +) varies horizontally with \( \rho \) in the phase planes of Figure
2.6 but the coexisting equilibrium (red \( \times \)) only changes vertically with \( \rho \) in Figure 2.6.
Therefore, as \( \rho \) increases from 0.1 to 0.26 (see Figures 2.6b and 2.6c), \( P^* \) is constant
while \( \bar{P} \) increases before the trajectory turns toward the coexisting equilibrium. There-
therefore, a “saddle point bloom” occurs as \( P \) is temporarily attracted toward \( \bar{P} \) and exceeds
\( P^* \). The bloom is terminated as \( P \) is repelled along the unstable manifold toward \( P^* \).
Thus, in the context of this model, a phytoplankton bloom is a rapid increase in phy-
toplankton concentration with an upper bound of \( \bar{P} \) that is not attained.

Supplemental movie 1 provides a phase plane animation of the non-autonomous
solution of equations (2.3) with \( \rho \) defined as in (2.11). The oscillation of the coefficient
\( \rho \) causes the coexisting equilibrium, the phytoplankton-only equilibrium, and the stable
manifold to move. This forces the trajectory of the solution, marked by a blue line, to
descend to the horizontal axis (the stable manifold of the saddle point phytoplankton-
only equilibrium), move along the horizontal axis toward the phytoplankton-only equi-
librium, and then move along the unstable manifold toward the coexisting equilibrium.
Although the coexisting equilibrium only moves vertically in the animation, the so-
lution initially moves down and to the left because it is trying to spiral toward the
coexisting equilibrium in a counter-clockwise manner (see Figure 2.6a).

2.5 Information from Linearization

To understand why the zooplankton are slow in responding to the phytoplankton
bloom (as in Figure 2.6b), system (2.3) is linearized about the phytoplankton-only
Figure 2.6: Illustration of the saddle point bloom mechanism. Phase plane trajectories of solutions of equations (2.3) using states of the system from the time series in Figure 2.5 as initial conditions. The dashed line in each plot is the unstable manifold of the phytoplankton-only equilibrium. The horizontal axis ($Z = 0$) is the stable manifold of the phytoplankton-only equilibrium. In (a), initial conditions correspond to day 80 of the non-autonomous solution (see Figure 2.5), and $\rho$ corresponds to day 130 of $\rho(t)$ from (2.11). As sunlight decreases, the solution spirals toward the coexisting equilibrium (red $\times$). In (b), initial conditions correspond to day 130 of the non-autonomous solution and $\rho$ corresponds to day 180 of $\rho(t)$ from (2.11). As sunlight gets low, zooplankton concentration gets low and the trajectory progresses slowly towards the coexisting equilibrium. In (c), initial conditions correspond to day 180 of the non-autonomous solution and $\rho$ corresponds to day 230 of $\rho(t)$ from (2.11). When zooplankton concentration is low and sunlight increases, a phytoplankton bloom develops.
equilibrium \((\bar{P}, 0)\). Abbreviating the system (2.3) as
\[
\frac{dP}{dt} = F(P, Z) \tag{2.12}
\]
\[
\frac{dZ}{dt} = G(P, Z),
\]
the linearization about \((\bar{P}, 0)\) yields a matrix equation whose matrix is the Jacobian
\[
J(\bar{P}, 0) = \begin{bmatrix}
J_{11} & J_{12} \\
0 & J_{22}
\end{bmatrix}
\tag{2.13}
\]
with
\[
J_{11} = \frac{\partial F}{\partial P} = \rho \mu_{\text{max}} \frac{(N_T - \bar{P})(k_N + N_T - \bar{P}) - k_N \bar{P}}{(k_N + N_T - \bar{P})^2} - m_P, \tag{2.14}
\]
\[
J_{12} = \frac{\partial F}{\partial Z} = -\frac{\rho \mu_{\text{max}} k_N}{(k_N + N_T - \bar{P})^2} \bar{P} - h_{\text{max}} \left(1 - e^{-a \bar{P}}\right), \tag{2.15}
\]
and
\[
J_{22} = \frac{\partial G}{\partial Z} = \alpha h_{\text{max}} \left(1 - e^{-a \bar{P}}\right) - m_Z, \tag{2.16}
\]
with \(\bar{P}\) defined as in (2.4). Since the matrix \(J(\bar{P}, 0)\) is triangular, its eigenvalues are the diagonal entries \(J_{11}\) and \(J_{22}\). Since the choice of \(\rho(t)\) from (2.11) and the chosen values for the other parameters assures \(\rho > \bar{P}_S\) (see top plot of Figure 2.5 and Condition 3 of section 2.4), it can be shown algebraically that \(J_{22} > 0\) and \(J_{11} < 0\). Therefore \(J_{11}\) is the eigenvalue corresponding to the stable manifold \(\{(P, Z) : Z = 0, 0 < P \leq N_T\}\) and \(J_{22}\) is the eigenvalue corresponding to the unstable manifold (the dashed line in each phase plane of Figure 2.6). As \(\rho\) decreases, \(J_{11}\) decreases monotonically and the \((P, Z)\) trajectory is placed closer to the horizontal axis (the stable manifold). The proximity of the trajectory to the horizontal axis places the trajectory under the temporary influence of the stable manifold. When \(J_{11}\) is low, it causes a slow progression of the trajectory along the horizontal axis. Therefore, the end of the trajectory in Figure 2.6b is still far away from the coexisting equilibrium.
2.6 Summary of Ordinary Differential Equations NPZ Model

A phytoplankton bloom can be simulated with system (2.3), shown again below, and an appropriate choice of the light response function $\rho$. The saddle point bloom mechanism described in section 2.4 explains in detail how the bloom initiates and terminates. Section 2.5 gives further details about the delayed zooplankton reaction which prolongs the bloom. Although predicted blooms from the system (2.3) using $\rho$ defined as in (2.11) initiate immediately following the winter solstice, which is inappropriate (too early for simulating spring blooms in the North Atlantic), the analytical results from system (2.3) are useful for understanding the dynamics of a more realistic reaction-diffusion NPZ model as discussed in chapter 3.

\[
\frac{dP}{dt} = \rho \mu_{max} \frac{N_T - P - Z}{k_N + N_T - P - Z} P - h_{max} (1 - e^{-aP}) Z - m_P P
\]

\[
\frac{dZ}{dt} = \alpha h_{max} (1 - e^{-aP}) Z - m_Z Z
\]
3.1 Construction of the Reaction-Diffusion NPZ Model

Predictions of equations (2.3) using \( \rho \) defined as in (2.11) produce a phytoplankton bloom that starts immediately after the winter solstice, see Figure 2.5. This is far earlier than the spring blooms in the North Atlantic start. This issue is addressed by incorporating physical driving forces into the model, drivers that have previously been used to explain phytoplankton blooms: diffusion and mixed layer depth. Despite the shortcomings of the ordinary differential equations model (2.2), (2.3), the study of its dynamical properties does inform the study of an analogous but spatial, reaction-diffusion system (3.1) with independent variable \( \xi \), representing depth.

\[
\begin{align*}
\partial_t P &= \rho e^{-kw\xi} \mu_{max} \frac{N}{k_N + N} P - h_{max} \left(1 - e^{-aP}\right) Z - m_P P + \partial_\xi (D \partial_\xi P) \\
\partial_t Z &= \alpha h_{max} \left(1 - e^{-aP}\right) Z - m_Z Z + \partial_\xi (D \partial_\xi Z) \\
\partial_t N &= -\rho e^{-kw\xi} \mu_{max} \frac{N}{k_N + N} P + (1 - \alpha) h_{max} \left(1 - e^{-aP}\right) Z + m_P P \\
&\quad + m_Z Z + \partial_\xi (D \partial_\xi N) \\
\rho(I) &= \frac{\Gamma I}{\sqrt{\mu_{max}^2 + \Gamma^2 I^2}} \\
D(\xi) &= D_{min} - \frac{D_{min} - D_{max}}{2} \left[1 + \tanh \left(\frac{M - \xi}{\psi}\right)\right] \\
D_{max} &= 10^{-2} M^2 \text{ day}^{-1}
\end{align*}
\]
The phytoplankton response to light is now given by the expression $\rho e^{-kW\xi}$ which accounts for light attenuating exponentially with depth. In (3.1), the expression for the parameter $\rho$, used in Kuhn et al. [35] and in Smith [67], is chosen for its ability to describe empirical data from natural populations of marine phytoplankton [68]. The diffusion coefficient $D(\xi)$, a simplified version of the diffusion coefficient from Gibson et al. [44], accounts for low diffusion in the lower ocean and higher diffusion in the upper mixed layer. Franks [69], and Brainerd and Gregg [70] reiterate the important difference between turbulence and mixing. In this dissertation, however, we make a simplifying assumption by using diffusion as a proxy for mixing resulting from turbulence. The upper mixed layer has diffusion $O(D_{\text{max}})$ and the lower ocean has diffusion $O(D_{\text{min}})$. $M$ is the mixed layer depth (i.e. the depth of the bottom of the upper mixed layer). The approximation for $D_{\text{max}}$ is like that of Kuhn et al. [35] but the coefficient $10^{-2}$ is chosen to keep $D_{\text{max}}$ in the range of diffusion levels suggested in Edwards et al. [53]. In this chapter, $\rho$, $M$, and $D_{\text{max}}$ are assumed constant in time. Seasonal changes in these three quantities are addressed in chapter 4. The parameter $\psi$ controls the thickness of the transition layer between the mixed layer and the lower ocean. We choose $\psi = 25$ m for a smooth transition from the mixed layer to the lower ocean. While very few papers have addressed this point, Gibson et al. [44] suggests $\Delta \xi = 5$ m but others have suggested a larger transition $O(25)$ m. This is computationally suitable for the vertical grid size of $\Delta \xi = 5$ m, which we use when we solve the system (3.1) in chapter 4. This vertical grid size was also chosen by Levy [36] and Kuhn et al. [35]. Furthermore, experiments with $\psi = 5$ m and $\Delta \xi = 1$ m did not significantly change the results. Table 3.1 gives the descriptions of and the values chosen for the parameters we have introduced to equations (2.3) by expanding it into the reaction-diffusion system (3.1). Figure 3.1 shows a profile of the depth-dependent solar radiation intensity and of the diffusion coefficient. The computational domain for depth $\xi$ is from 0 to 350 meters, as in Levy [36], to accommodate for most values of $M$. As in chapter 2, let $N_T = N + P + Z$. Initial conditions of $N_T$ are assumed to be constant with depth. Summing the equations (3.1), $N_T$ satisfies $\partial_t N_T = \partial_\xi (D \partial_\xi N_T)$. We impose no-flux
Table 3.1: Parameter descriptions and values introduced in equations (3.1). * Value chosen for a smooth transition from mixed layer to lower ocean.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Gamma$</td>
<td>Initial photosynthetic slope</td>
<td>0.055 [35]</td>
<td>(E m$^{-1}$)$^{-1}$day$^{-1}$</td>
</tr>
<tr>
<td>$k_W$</td>
<td>Light attenuation constant</td>
<td>0.06 [53]</td>
<td>m$^{-1}$</td>
</tr>
<tr>
<td>$\psi$</td>
<td>Transition layer parameter</td>
<td>25*</td>
<td>m</td>
</tr>
<tr>
<td>$D_{min}$</td>
<td>Diffusion level in the lower ocean</td>
<td>$10^{-5}$ [44]</td>
<td>m$^2$s$^{-1}$</td>
</tr>
<tr>
<td>$H$</td>
<td>Water column depth</td>
<td>350</td>
<td>m</td>
</tr>
</tbody>
</table>

boundary conditions at the top and bottom boundaries. Since $N_T$ is independent of $\xi$ initially, then as a solution of the diffusion equation with no-flux boundary conditions, $N_T$ is also independent of $\xi$ for all time, and thus is constant in time and space. So as in chapter 2, $N_T$ is constant. Therefore, for no-flux boundary conditions and spatially independent initial conditions, $N_T = \frac{1}{H} \int_0^H (P + Z + N) d\xi = N_T$, a constant. Writing system (3.1) in simplified form

$$\partial_t u = \partial_\xi (D \partial_\xi u) + f(u),$$  \hspace{1cm} (3.2)

where $u = (P, Z, N)$, the system is solved using a Crank-Nicolson [71] scheme

$$\frac{u_j^{n+1} - u_j^n}{\Delta t} = \frac{1}{2\Delta \xi^2} \left[ D_{j+1/2}^n (u_{j+1}^n - u_j^n) - D_{j-1/2}^n (u_j^n - u_{j-1}^n) \right] + D_{j+1/2}^{n+1} (u_{j+1}^{n+1} - u_j^{n+1}) - D_{j-1/2}^{n+1} (u_j^{n+1} - u_{j-1}^{n+1}) + f(u_j^n)$$  \hspace{1cm} (3.3)

for time step $n$ and depth step $j$. See appendix A for more details.

### 3.2 Linearizing the Reaction-Diffusion Model and Finding the Equilibria

To begin the stability analysis of the reaction-diffusion system (3.1), the system is reduced to two differential equations. Since, as noted above, $N_T$ is constant in time and space, we can reduce the system of three equations (3.1) to two (3.4), similar to the change carried out in chapter 2 converting the system (2.2) to (2.3).
Figure 3.1: Depth profile of actual solar radiation intensity (solid black) and diffusion coefficient (dashed blue) with constant surface solar radiation intensity $I = 50 \text{ Em}^{-2}\text{d}^{-1}$, $k_W = 0.02 \text{ m}^{-1}$, $D_{\text{max}} = 10^{-3} \text{ m}^2\text{s}^{-1}$ and mixed layer depth $M = 100 \text{ m}$ for purposes of illustration. Light attenuates exponentially with depth. The mixed layer depth $M$ is at the inflection point of the diffusion profile and at the center of the transition layer. $M$ varies seasonally and geographically and typically ranges from 20 to 300 meters.
\[
\begin{align*}
\frac{\partial_t P}{\partial_t Z} &= \rho e^{-kW\mu_{\max}} \frac{N_T - P - Z}{k_N + N_T - P - Z} P - h_{\max} (1 - e^{-aP}) Z - m_P P + \partial_\xi (D \partial_\xi P) \\
\frac{\partial_t Z}{\partial_t Z} &= \alpha h_{\max} (1 - e^{-aP}) Z - m_Z Z + \partial_\xi (D \partial_\xi Z) \\
D(\xi) &= D_{\min} - \frac{D_{\min} - D_{\max}}{2} \left[ 1 + \tanh \left( \frac{M - \xi}{\psi} \right) \right]
\end{align*}
\]

For the remainder of this chapter, we assume \( \rho \) and \( D \) are constant in time although this restriction will be lifted in Chapter 4 where we use actual seasonal data.

To linearize the system (3.4), let \((\tilde{P}(\xi), \tilde{Z}(\xi))\) be an equilibrium of (3.4) and \((P', Z')\) be a “perturbation” of the equilibrium. Define \(P'(\xi, t) = \tilde{P}(\xi)e^{\lambda t}\) and \(Z'(\xi, t) = \tilde{Z}(\xi)e^{\lambda t}\) with amplitudes \(\tilde{P}\) and \(\tilde{Z}\), as in Edwards et al. [53], such that

\[
\begin{align*}
P'(\xi, t) &= P(\xi, t) - \tilde{P}(\xi), \text{ and} \\
Z'(\xi, t) &= Z(\xi, t) - \tilde{Z}(\xi).
\end{align*}
\]

If the system (3.4) is abbreviated as

\[
\begin{align*}
\frac{\partial_t P}{\partial_t Z} &= F(P, Z) + \partial_\xi (D \partial_\xi P) \\
\frac{\partial_t Z}{\partial_t Z} &= G(P, Z) + \partial_\xi (D \partial_\xi Z)
\end{align*}
\]

then it can be written that
\[ \lambda \dot{P} e^{\lambda t} = \partial_t P \]
\[ = F(P, Z) + \partial_\xi (D\partial_\xi P) \]
\[ = F(\tilde{P} + P', \tilde{Z} + Z') + \partial_\xi (D\partial_\xi (\tilde{P} + P')) \]
\[ = F(\tilde{P}, \tilde{Z}) + P'\partial_p F(\tilde{P}, \tilde{Z}) + Z'\partial_Z F(\tilde{P}, \tilde{Z}) + \partial_\xi (D\partial_\xi (\tilde{P} + P')) + \mathcal{O}((P')^2, (Z')^2, P'Z') \]
\[ \approx F(\tilde{P}, \tilde{Z}) + \partial_\xi (D\partial_\xi \tilde{P}) + P'\partial_p F(\tilde{P}, \tilde{Z}) + Z'\partial_Z F(\tilde{P}, \tilde{Z}) + \partial_\xi (D\partial_\xi P') \]
\[ = \dot{P}(\xi)e^{\lambda t}\partial_p F(\tilde{P}, \tilde{Z}) + \dot{Z}(\xi)e^{\lambda t}\partial_z F(\tilde{P}, \tilde{Z}) + e^{\lambda t}\partial_\xi (D\partial_\xi \tilde{P}). \]

Therefore,
\[ \partial_p F(\tilde{P}, \tilde{Z}) \dot{P} + \partial_z F(\tilde{P}, \tilde{Z}) \dot{Z} + \partial_\xi (D\partial_\xi \tilde{P}) = \lambda \dot{P}, \quad (3.6) \]

and similarly,
\[ \partial_p G(\tilde{P}, \tilde{Z}) \dot{P} + \partial_z G(\tilde{P}, \tilde{Z}) \dot{Z} + \partial_\xi (D\partial_\xi \tilde{Z}) = \lambda \dot{Z}. \quad (3.7) \]

Equations (3.6) and (3.7) can be written as a matrix equation
\[
\begin{bmatrix}
\left. \frac{\partial F}{\partial P} \right|_{(\tilde{P}, \tilde{Z})} + \left. \frac{\partial}{\partial \xi} \left( D \frac{\partial}{\partial \xi} \right) \right|_{(\tilde{P}, \tilde{Z})} & \left. \frac{\partial F}{\partial Z} \right|_{(\tilde{P}, \tilde{Z})} \\
\left. \frac{\partial G}{\partial P} \right|_{(\tilde{P}, \tilde{Z})} & \left. \frac{\partial G}{\partial Z} \right|_{(\tilde{P}, \tilde{Z})} + \left. \frac{\partial}{\partial \xi} \left( D \frac{\partial}{\partial \xi} \right) \right|_{(\tilde{P}, \tilde{Z})}
\end{bmatrix}
\begin{bmatrix}
\dot{P} \\
\dot{Z}
\end{bmatrix}
= \lambda
\begin{bmatrix}
\dot{P} \\
\dot{Z}
\end{bmatrix}. \quad (3.8)
\]

The stability of the equilibrium calculated depends on the eigenvalues \( \lambda_j, j = 1, \ldots, 2m \), of the Jacobian matrix in equation (3.8). Since we calculate the equilibria numerically then we must discretize the depth of the water column (i.e. choose a finite number of depth values \( \xi_j, j = 1, \ldots, m \), for which to approximate the value of the equilibria). Construction of the full, depth-coupled \( 2m \times 2m \) Jacobian matrix
is discussed in Appendix B. If the real part of every eigenvalue $\lambda_j$ for an equilibrium $(\tilde{P}, \tilde{Z})$ is negative, then the equilibrium is asymptotically stable. If even one eigenvalue has a positive real part, then the equilibrium is unstable. The linear stability of an equilibrium can quickly be determined by checking whether the largest real part of the eigenvalues is positive ($\max_j \Re(\lambda_j) > 0$) or negative ($\max_j \Re(\lambda_j) < 0$).

The depth-dependent equilibria of equations (3.4) are computed using the technique from Edwards et al. [53]. After discretizing depth, we create an initial guess by calculating the equilibrium $(\tilde{P}_j, \tilde{Z}_j)$ at each depth $\xi_j$, $j = 1, \ldots, m$, with $D \equiv 0$ (i.e. we analytically calculate the equilibrium for (3.9)).

$$\frac{dP_j}{dt} = \rho e^{-kw\xi_j} \mu_{max} \frac{N_T - P_j - Z_j}{k_N + N_T - P_j - Z_j} P_j - h_{max} (1 - e^{-aP_j}) Z_j - m_P P_j$$

$$\frac{dZ_j}{dt} = \alpha h_{max} (1 - e^{-aP_j}) Z_j - m_Z Z_j$$

(3.9)

We define $\vec{P}$ and $\vec{Z}$ as the vectors with entries $\tilde{P}_j$ and $\tilde{Z}_j$ ($j = 1, \ldots, m$), respectively. Using $(\vec{P}, \vec{Z})$ as an initial guess, we use fsolve in MATLAB to solve the system (3.10).

$$F(P, Z) + \partial_\xi (D \partial_\xi P) = 0$$

$$G(P, Z) + \partial_\xi (D \partial_\xi Z) = 0$$

(3.10)

Figure 3.2 shows the depth profiles of the initial guess and the computed coexisting equilibrium of (3.4) using $\rho = 1$ and a mixed layer depth of 100 m.

### 3.3 Linear Stability of the Unforced Reaction-Diffusion NPZ Model

We investigate the effects of the parameters $\rho$ (response to solar radiation), $M$ (mixed layer depth), and $D_{max}$ (mixed layer diffusion) on the equilibria of the space dependent, unforced system (3.4), which are calculated using the technique from the section 3.2. Stability diagrams (Figure 3.3) are constructed for the unforced system such that $\rho$ is plotted against either $M$ or $D_{max}$. All other parameters assume the values listed in Tables 2.1 and 3.1. The white (left) region is where the plankton-free equilibrium is stable. The aqua (middle) region is where the phytoplankton-only
equilibrium is stable. The yellow (right) region is where the coexisting equilibrium is stable. No regions were found where the coexisting equilibrium is unstable (Figure 2.3d). Edwards et al. [53] found a large region where the coexisting equilibrium is unstable when plotting $h_{\text{max}}$ against diffusion $D$, where $D$ is constant in time and depth. However, the region of instability for the coexisting equilibrium in their study is in areas where $h_{\text{max}} > 1.5 \, \text{d}^{-1}$ and $D < 10^{-5} \, \text{m}^2\text{s}^{-1}$, which is mostly outside the range of these parameters used in this dissertation. We observed that the introduction of a depth dependent diffusion coefficient in this model is associated with the absence of unstable coexisting equilibria.

The construction of these diagrams begins with computing the largest real part of the eigenvalues $\lambda_j$, $j = 1, \ldots, 2m$, from equation (3.8) for each pair of values $\rho$ and $M$ (or $\rho$ and $D_{\text{max}}$) for the linearization about the plankton-free equilibrium. The borderline between the white (left) region and the aqua (middle) region represents the border between the plankton-free equilibria in which $\max_j \Re(\lambda_j) < 0$ (stable) and the plankton-free equilibria in which $\max_j \Re(\lambda_j) > 0$ (unstable). In other words, it is the contour line where $\max_j \Re(\lambda_j) = 0$. Next, equation 3.4 is linearized about the phytoplankton-only equilibrium. The borderline between the aqua (middle) region...
and the yellow (right) region represents the border between the phytoplankton-only equilibria in which \( \max_j \Re(\lambda_j) < 0 \) (stable) and the phytoplankton-only equilibria in which \( \max_j \Re(\lambda_j) > 0 \) (unstable). Separate stability diagrams for the coexisting equilibrium (not shown) were constructed. No regions of instability (i.e. behavior like in Figure 2.3d) were found. Therefore, for the stability diagrams in this dissertation, the coexisting equilibrium is stable whenever the plankton-free equilibrium and the phytoplankton-only equilibrium are unstable (yellow, or left, region). A depth grid size of \( \Delta \xi = 1 \) meter was chosen for the stability diagrams; the choice of \( \Delta \xi = 5 \) meters is too coarse to obtain reliable stability diagrams.

Figure 3.3 illustrates the importance of the parameters for light response \( \rho \), mixed layer depth \( M \) and mixed layer diffusion \( D_{\text{max}} \) for understanding this model. Figure 3.3a, c, e, show \( \rho \) plotted against \( M \) for \( D_{\text{max}} \) values \( 10^{-2} \), \( 10^{-3} \) and \( 10^{-4} \) m\(^2\) s\(^{-1}\), respectively. A typical value for the Gulf of Alaska in spring is \( D_{\text{max}} = 10^{-3} \) m\(^2\) s\(^{-1}\) [44]. The influence of the mixed layer depth on the stability of the equilibria increases with mixed layer diffusion. Mixed layer depth has less influence on the selection of the stable state when \( D_{\text{max}} = 10^{-4} \) m\(^2\) s\(^{-1}\) except when \( M \) is small (Figure 3.3e) but shows greater influence when \( D_{\text{max}} = 10^{-2} \) m\(^2\) s\(^{-1}\) (Figure 3.3a). Evidently, mixed layer depth has little influence except if it is very small or if \( D_{\text{max}} \) is quite large. However, Figure 3.3b, d, f show that both \( \rho \) and \( D_{\text{max}} \) significantly influence which of the three equilibria is stable, regardless of the mixed layer depth.

The dashed lines represent seasonal increases of light response for moderate levels of mixed layer depth (or mixed layer diffusion) as winter progresses into summer. For each trajectory, the left end of the dashed line represents the winter solstice (when the solar radiation is at, say, 20 percent of the assumed seasonal maximum which is typical in the North Atlantic, 40-45°N). The right arrow on the right end of the dashed line represents the summer solstice. In Figure 3.3b, d, f, we see that when \( D_{\text{max}} = 10^{-2} \), the phytoplankton-only equilibrium gains its stability at a higher light response value than it does when \( D_{\text{max}} = 10^{-3} \). In Figure 3.3e we see that the coexisting equilibrium remains stable year-round, regardless of the mixed layer depth. In Figure 3.3a, c, we
see that when $M = 150$ m, the phytoplankton-only equilibrium gains its stability at a higher light response value than it does when $M = 25$ m. However, when $D_{\text{max}} = 10^{-3}$ (Figure 3.3c) the phytoplankton-only equilibrium gains its stability at the same light response value for any mixed layer depth deeper than 100 meters.

The stability diagrams in Figure 3.3 can indicate which ecological theories are credible for planktonic ecosystems with certain parameter regimes. For instance, one may consider using equations (3.4) to simulate seasonal phytoplankton blooms. As discussed in section 1.5, Behrenfeld and Boss [54] suggest that blooms represent a change from one ecological state to another. Figure 3.3 shows that the model (3.4) can change between three states (stable plankton-free equilibrium, stable phytoplankton-only equilibrium, or stable coexisting equilibrium) as light response, mixed layer depth and mixed layer diffusion change. Now, consider the equations (3.4) with the addition of seasonally dependent light response $\rho$ and mixed layer depth $M$, and constant mixed layer diffusion $D_{\text{max}}$. Choosing a high value of mixed layer diffusion such as $D_{\text{max}} = 10^{-2}$ m$^2$ d$^{-1}$ causes the mixed layer depth to have a significant influence on which equilibrium is the attractor, as shown in Figure 3.3a. A key assumption of Sverdrup’s Critical Depth Hypothesis [11] is that the mixed layer be characterized by high turbulence. If this is the case, then Sverdrup suggests that changing mixed layer depth is the primary driving force behind the annual North Atlantic spring phytoplankton bloom. However, choosing a low value of mixed layer diffusion, such as $D_{\text{max}} = 10^{-4}$ m$^2$d$^{-1}$ (Figure 3.3e) or $D_{\text{max}} = 10^{-3}$ m$^2$ d$^{-1}$ (Figure 3.3c), causes the mixed layer depth to have minimal (if any) effect on which equilibrium is attracting. Similar to Sverdrup, we suggest that only at high levels of diffusion does the mixed layer depth strongly influence which stable state of the ecosystem is attracting. The mechanisms attracting plankton populations that occur in low diffusion environments are congruent with the Critical Turbulence Hypothesis [10]. According to this theory, if the ratio of mixed layer diffusion rate and growth rate is low, a phytoplankton population will be maintained, regardless of the mixed layer depth. Thus, the solution will be attracted to stable states with phytoplankton, which are the yellow (right) and aqua (middle)
Figure 3.3: Assuming parameter values from Tables 2.1 and 3.1 except where otherwise labeled, stability diagrams of equations (3.4). In (a), (c) and (e) mixed layer depth is plotted against light response with each diagram corresponding to a different, fixed value of $D_{max}$. In (b), (d) and (f) mixed layer diffusion is plotted against light response with each diagram corresponding to a different, fixed value of $M$. White (left) region: plankton-free equilibrium is stable, Aqua (middle) region: phytoplankton-only equilibrium is stable, Yellow (right) region: coexisting equilibrium is stable. Dashed lines represent seasonal increases of light response, with the summer solstice at right arrow, for a certain level of mixed layer depth or mixed layer diffusion.
regions in Figure 3.3.

Figure 3.4 shows three stability diagrams with $\rho$ plotted against $M$ and three stability diagrams with $\rho$ plotted against $D_{\text{max}}$ as in Figure 3.3 but with the light attenuation coefficient $k_W$ reduced from 0.06 to 0.02 m$^{-1}$. These values approximate the seasonal range of $k_W$ in the North Atlantic open ocean as can be observed at https://oceancolor.gsfc.nasa.gov/. This increases the light availability in the water column which reduces the area of the stable plankton-free equilibrium and increases the area of the stable coexisting equilibrium. This is expected because in equation (3.4) growth rate is related to light availability. Therefore, increased light availability boosts the phytoplankton growth rate. This in turn increases the phytoplankton population, providing more prey for zooplankton, which facilitates the stability of the coexisting equilibrium. Reducing $k_W$ “brightens” the ocean, roughly translating the regions of stability toward the left. Recall that the parameter values in Table 2.1 cause the phytoplankton-only equilibrium of the ordinary differential equations (2.3) to be stable for $0.075 < \rho < 0.078$. Figures 3.4e and 3.4f show that for low values of $M$, $D_{\text{max}}$, and $k_W$ (as compared with Figures 3.3e and 3.3f), the phytoplankton-only equilibrium of the partial differential equations (3.4) is stable when the value of $\rho$ is within a small interval about a value less than 0.1. Thus, as the values of $M$, $D_{\text{max}}$, and $k_W$ approach 0, the predictions of the partial differential equations (3.4) agree with the predictions of the ordinary differential equations (2.3) for low to moderate $\rho$ (see Figure 2.3). However, for larger $\rho$ in system (3.4), we never see unstable coexisting equilibria.

Figure 3.5 shows three stability diagrams with $\rho$ plotted against $M$ and three stability diagrams with $\rho$ plotted against $D_{\text{max}}$ as in Figure 3.3 but with the maximum grazing rate $h_{\text{max}}$ reduced from 1.5 to 0.5 d$^{-1}$, the value chosen by Busenberg et al. [52]. This enlarges the region of stability for the phytoplankton-only equilibrium as we expect from the discussion of the $\bar{P}_S$ parameter in section 2.3. Consequently, reducing the maximum grazing rate $h_{\text{max}}$ causes the phytoplankton-only equilibrium to be stable for a higher value of light response $\rho$. As can be seen from the second equation in (2.2), a lower value of $h_{\text{max}}$ requires a higher phytoplankton concentration.
Figure 3.4: Stability diagrams of equations (3.4) with parameter values from Tables 2.1 and 3.1 except where otherwise labeled. The diagrams are equivalent to those of Figure 3.3 except that $k_{W}$ is reduced from 0.06 to 0.02 m$^{-1}$. In (a), (c) and (e) mixed layer depth is plotted against light response with each diagram corresponding to a different, fixed value of $D_{\text{max}}$. In (b), (d) and (f) mixed layer diffusion is plotted against light response with each diagram corresponding to a different, fixed value of $M$. White (left) region: plankton-free equilibrium is stable, Aqua (middle) region: phytoplankton-only equilibrium is stable, Yellow (right) region: coexisting equilibrium is stable. Dashed lines represent seasonal increases of light response, with the summer solstice at right arrow, for a certain level of mixed layer depth or mixed layer diffusion.
for the zooplankton growth term $\alpha h_{\text{max}}(1-e^{-aP})Z$ to be larger than the zooplankton loss term $m_ZZ$. In other words, a system with a lower maximum grazing rate requires a larger phytoplankton population (facilitated by increased sunlight) to sustain the zooplankton population.

The stability diagrams in Figure 3.5 offer further insight from the discussion of Figure 3.3. Again, consider equations (3.4) with seasonally dependent light response $\rho$ and mixed layer depth $M$ (or mixed layer diffusion $D_{\text{max}}$). Imagine now tracing increasing seasonal light along the arrow in Figure 3.5b, when the mixed layer is deep. The widening of the phytoplankton-only stability region forces this equilibrium to remain stable over more light values, which is a proxy for time in a seasonal cycle. Revisiting Behrenfeld and Boss’ [54] suggestion that blooms result from transitioning from one attracting ecological equilibrium to another, we suggest that Figure 3.5 shows that decreased grazing rates lead to a larger region of stability for the phytoplankton-only states. We believe this is analogous to the Dilution-Recoupling Hypothesis [8], where increased mixed layer depth and vertical diffusion reduces the contact rates and therefore grazing rates between zooplankton and phytoplankton. Lower grazing rates increase the area where the phytoplankton-only equilibrium is an attractor, therefore leading to a bloom. Likewise, Behrenfeld and Boss [54] suggest that high-latitude blooms must follow from winter decimation of zooplankton, thus lowering grazing rates. This decimation might be the result of the ecosystem briefly entering a state in the winter where the phytoplankton-only equilibrium is attracting. The ecosystem then quickly returns to a state where the coexisting equilibrium is attracting so that the zooplankton population does not decline to a point from which it cannot recover. Although the equilibria influence the ecosystem, seasonally changing environmental conditions prevent the system from achieving any of the equilibrium states as explained by Hutchinson [72]. The region of stability for the phytoplankton-only equilibrium is very narrow for high values of maximum grazing rate $h_{\text{max}}$ as seen in Figure 3.3 and Figure 3.4. Ecosystems with parameterizations like that of Figure 3.3 or Figure 3.4
would not tend toward a phytoplankton-only equilibrium for long. Plankton populations in sufficiently low sunlight and high mixed layer diffusion (or deep mixed layer depth) would no longer be attracted by a stable coexisting equilibrium but be attracted by a plankton-free state only after a brief attraction by a phytoplankton-only equilibrium. Intuitively, these are not ideal conditions for facilitating a phytoplankton bloom. Therefore, it is appropriate that equations (3.4) be parameterized so that the model has a sufficiently large region of stability for the phytoplankton-only equilibrium.

3.4 Limitations of the Reaction-Diffusion NPZ Model

The simplicity of the reaction-diffusion model in this dissertation calls for caution when interpreting its results. The model does not account for sinking of phytoplankton or detritus, which occurs in nature. The model also does not account for the deepening of the mixed layer causing the entrainment of nutrients from the depths into the euphotic zone. The assumption that \( N + P + Z = N_T \) is a constant, \( N_T \), implies that no nitrogen leaves the upper ocean, where the biological interactions between nutrients, phytoplankton, and zooplankton occur. If sinking of phytoplankton (or detritus) and entrainment of nutrients into the euphotic zone were to be incorporated, then the value of \( N_T \) would change accordingly. It is reasonable to expect that changing values of \( N_T \), resulting from sinking phytoplankton and nutrient entrainment, would alter the equilibria of the reaction-diffusion model. However, based on the analysis of Busenberg et al. [52] and the analysis of this dissertation, it is also reasonable to expect that the reaction-diffusion model will always have the same three equilibria (plankton-free, phytoplankton-only, and coexisting), regardless of the value of \( N_T \). It is also assumed in this dissertation that \( N_T \) is constant with depth, which is not so in the ocean. However, time-dependent depth profiles of \( N_T \) would be difficult to estimate and would complicate the process of solving the equations of the system. Nevertheless, valuable insights are gained from studying the reaction-diffusion system with temporally and spatially constant \( N_T \).
Figure 3.5: Stability diagrams of equations (3.4) with parameter values from tables 2.1 and 3.1 except where otherwise labeled. The diagrams are equivalent to those of Figure 3.3 except that $h_{max}$ is reduced from 1.5 to 0.5 d$^{-1}$. In (a), (c) and (e) mixed layer depth is plotted against light response with each diagram corresponding to a different, fixed value of $D_{max}$. In (b), (d) and (f) mixed layer diffusion is plotted against light response with each diagram corresponding to a different, fixed value of $M$. White (left) region: plankton-free equilibrium is stable, Aqua (middle) region: phytoplankton-only equilibrium is stable, Yellow (right) region: coexisting equilibrium is stable. Dashed lines represent seasonal increases of light response, with the summer solstice at right arrow, for a certain level of mixed layer depth or mixed layer diffusion.
3.5 Attracting/Repelling Bloom Behavior in a Reaction-Diffusion NPZ Model

The reaction-diffusion system has a mechanism similar to the attracting/repelling saddle point bloom mechanism of the system of ordinary differential equations (2.3). To demonstrate the mechanism in the reaction-diffusion system, a coexisting equilibrium state of (3.4) subject to low (winter-level) sunlight is used as initial conditions. Such an equilibrium has a low concentration of zooplankton. Then the autonomous system (3.4) is solved subject to higher (summer-level) sunlight. The solution is expected to include a phytoplankton bloom like in Figure 2.5.

The techniques of section 3.2 are utilized to compute the equilibrium to be used for initial conditions. The parameter $\rho$ is set to 0.35 and for illustrative purposes, $h_{\text{max}}$ is set to 0.75 d$^{-1}$ and $k_W$ is set to 0.06 m$^{-1}$. Mixed layer depth $M$ is set to 130 m, which is a common winter value in the North Atlantic, and $D_{\text{max}} = 10^{-3}$ m$^2$ s$^{-1}$, which is in the upper range of diffusion values in Edwards et al. [53]. Figure 3.6a shows depth profiles of the computed coexisting equilibrium of system (3.4) with $\rho = 0.35$, $h_{\text{max}} = 0.75$ d$^{-1}$, $M = 130$ m, and $D_{\text{max}} = 10^{-3}$ m$^2$ s$^{-1}$. The zooplankton concentration is low at all depths in the water column, a prime condition for a bloom to begin. This equilibrium is used as the initial condition for system (3.4) with the same parameterization but now $\rho$ is set to 1. Figure 3.6b shows the depth profile of the coexisting equilibrium with the same parameterization as Figure 3.6a except now $\rho = 1$. In this case, the solution of (3.4) is expected to converge to the equilibrium in Figure 3.6b.

Figure 3.7 shows the predicted surface concentrations as a function of time for 90 days as predicted by the autonomous system (3.4) with $\rho \equiv 1$ and initial conditions as shown in Figure 3.6a. As expected, the phytoplankton bloom before the system subsides to the coexisting equilibrium state in Figure 3.6b.

Figure 3.8 shows the phytoplankton depth profiles from days 1, 10, 30, and 50 (out of 90 days) of the solution shown in Figure 3.7 along with the phytoplankton depth profiles from the phytoplankton-only equilibrium and coexisting equilibrium with
Figure 3.6: Depth profiles of the coexisting equilibrium for system (3.4) with $D_{\text{max}} = 10^{-3}$ m$^2$s$^{-1}$, $M = 130$ m, and $h_{\text{max}} = 0.75$ d$^{-1}$. In (a), $\rho = 0.35$ and in (b), $\rho = 1$.

Figure 3.7: Phytoplankton and zooplankton surface concentrations computed from the depth dependent equations (3.4) with $D_{\text{max}} = 10^{-3}$ m$^2$s$^{-1}$, $M = 130$ m, $h_{\text{max}} = 0.75$ d$^{-1}$, and $\rho = 1$, and initial conditions as shown in Figure 3.6a and conditions on day 90 shown in Figure 3.6b.
$M = 130$ m, and $D_{\text{max}} = 10^{-3}$ m$^2$s$^{-1}$, $h_{\text{max}} = 0.75$ d$^{-1}$, and $\rho = 1$. On day 1 (Figure 3.8a), the phytoplankton concentration is relatively low at all depths and close to the phytoplankton depth profile of the coexisting equilibrium. On day 10 (Figure 3.8b), the phytoplankton concentration at all depths has risen relatively close to the levels of the phytoplankton depth profile of the phytoplankton-only equilibrium. Figure 3.7 shows that on day 10, the surface phytoplankton is near its peak concentration. On day 30 (Figure 3.8c), the phytoplankton concentration at all depths has fallen to levels close to the corresponding levels of the phytoplankton depth profile of the coexisting equilibrium. In Figure 3.7, the surface phytoplankton concentration on day 30 has fallen just below what appears to be its level in a coexisting equilibrium state; the system appears to essentially achieve this coexisting equilibrium by day 90. On day 50 (Figure 3.8d), the phytoplankton concentration at all depths almost matches the corresponding levels of the phytoplankton depth profile of the coexisting equilibrium. Accordingly, the surface phytoplankton concentration in Figure 3.7 also appears to be very close to its level in the coexisting equilibrium on day 50. Thus in the context of this reaction-diffusion NPZ model, a phytoplankton bloom is a rapid increase in phytoplankton concentration with an upper bound of the phytoplankton-only equilibrium at all depths that is not attained. Evidently, when the coexisting equilibrium of the NPZ reaction-diffusion system (3.4) is stable and given a change in $\rho$, the phytoplankton-only equilibrium has a temporary attracting behavior that causes phytoplankton blooms in a manner analogous to the way the phytoplankton-only equilibrium causes blooms in the system of ordinary differential equations (2.3). A key difference is that the attracting states of the reaction-diffusion NPZ model are influenced not only by seasonally changing solar radiation, but also by diffusion, and by mixed layer depth [55].

Supplemental movie 2 provides a depth profile animation of the phytoplankton predictions of equations (3.4) with initial conditions $(P(\xi), Z(\xi))$ from Figure 3.6a and $\rho = 1$. The low initial zooplankton concentration and high sunlight intensity cause the phytoplankton depth profile to move toward the phytoplankton-only equilibrium depth.
Figure 3.8: Depth profiles of the phytoplankton component of the phytoplankton-only equilibrium and coexisting equilibrium of the system (3.4) with $M = 130$ m, $D_{max} = 10^{-3}$ m$^2$s$^{-1}$, $h_{max} = 0.75$ d$^{-1}$, and $\rho = 1$ along with depth profiles of the solution of (3.4): day 1 (a), day 10 (b), day 30 (c), and day 50 (d).
profile. Then the phytoplankton depth profile turns toward the coexisting equilibrium depth profile and converges to it.
Chapter 4

EVALUATION OF THE ATTRACTING/REPELLING MECHANISM FOR DESCRIBING BLOOMS IN THE NORTH ATLANTIC

4.1 Description of North Atlantic Data and its Use

In system (3.1), solar radiation data is incorporated to describe the quantity $I(t)$ and mixed layer depth data is used to describe the quantity $M(t)$. The satellite data PAR (Photosynthetically Active Radiation) and chl-ocx (chlorophyll) collected by the NASA MODIS-Aqua satellite is used. The PAR and chlorophyll data are available at https://oceancolor.gsfc.nasa.gov/. The mixed layer depth data is retrieved from HYCOM (HYbrid Coordinate Ocean Model) at https://hycom.org/. The region 25-35°W, 40-45°N in the North Atlantic Ocean is investigated. Time series of the horizontally averaged PAR and chlorophyll data from 2009 through 2015 are used for this region.

4.2 Analysis of North Atlantic Bloom Simulations

The predictions of model surface concentrations of phytoplankton from equations (3.1), using PAR data for $I(t)$ and mixed layer depth data for $M(t)$, are compared to a time series of the chlorophyll data. In this chapter, initial conditions for system (3.1) are set to $P(\xi) \equiv 0.2$ mmol N m$^{-3}$, $Z(\xi) \equiv 0.2$ mmol N m$^{-3}$, and $N(\xi) \equiv 1.6$ mmol N m$^{-3}$. These three values were selected by Gentleman and Neuheimer [61] for their ordinary differential equations NPZ model. For the parameter ranges chosen in this dissertation, the solution of system (3.1) becomes periodic after the first year. Therefore, only the part after the first year is shown. A time step of $\Delta t = 0.1$ days and a depth grid size of $\Delta \xi = 5$ meters are chosen to conserve the total nitrogen in the system. A grid size of $\Delta \xi = 1$ meter requires a smaller time step and, consequently,
longer running time for the numerical scheme described in appendix A. We have found that solutions of system (3.1) with $\Delta \xi = 5$ meters are essentially the same as solutions with $\Delta \xi = 1$ meter. Figure 4.1 shows the predictions of the system (3.1) on the North Atlantic region, using parameter values in Tables 2.1 and 3.1 except for $h_{\text{max}} = 0.5$ d$^{-1}$ and $k_W = 0.02$ m$^{-1}$. The value of $h_{\text{max}}$ is reduced from its value in Table 2.1 to broaden the region of stability of the phytoplankton-only equilibrium (as shown in Figure 3.5). $D_{\text{min}}$ is reduced to $10^{-6}$ m$^2$s$^{-1}$ in order to remain well below $D_{\text{max}}(t) = 10^{-2}M(t)^2$ day$^{-1}$. Sinusoidal best-fit approximations ($\alpha_1 + \alpha_2 \cos\left(\frac{2\pi}{365} t\right) + \alpha_3 \sin\left(\frac{2\pi}{365} t\right)$ for weights $\alpha_1$, $\alpha_2$ and $\alpha_3$) for PAR and mixed layer depth, shown in Figure 4.1, are used to describe the quantities $I(t)$ and $M(t)$, respectively, to avoid noise in the solution. In the second plot from the bottom, it is seen that the model phytoplankton blooms start and end too early, but the model phytoplankton curve otherwise follows the increases and decreases in the chlorophyll time series relatively well. The bottom plot shows that the surface phytoplankton (prey) concentration remains at least as high as the surface zooplankton (predator) concentration, which makes biological sense.

To study the effect of PAR, diffusion and mixed layer depth data on the dynamics of the model equations (3.4), we construct stability plots as is done in section 3.3. Figure 4.2 is a stability diagram constructed for system (3.4) with the same parameter values used to produce the results in Figure 4.1. The parameter $\rho$ is plotted against $D_{\text{max}}$ to show the regions of stability for the plankton-free equilibrium, the phytoplankton-only equilibrium and the coexisting equilibrium. The white (left) region is where the plankton-free equilibrium is stable. The aqua (middle) region is where the phytoplankton-only equilibrium is stable. The yellow (right) region is where the coexisting equilibrium is stable. No regions were found where the coexisting equilibrium exists and is unstable. The dashed curve is the seasonal trajectory of sinusoidal approximations for light response $\rho$ and upper mixed-layer diffusion $D_{\text{max}}$. This diagram and Figure 4.4 are constructed using the techniques from section 3.3. Figure 4.2 shows that the $D_{\text{max}}$ verses $\rho$ trajectory lands close to the border between the region of stability for the phytoplankton-only equilibrium and the region of stability.
Figure 4.1: Time series of solution of system (3.1) with $I(t)$ described by PAR data and $M(t)$ described by mixed layer depth data. All data averaged over the region 40-45°N, 25-35°W in the North Atlantic. Parameter values from Table 2.1 and Table 3.1 except for $k_W = 0.02$ m$^{-1}$, $D_{min} = 10^{-6}$ m$^2$s$^{-1}$, and $h_{max} = 0.5$ d$^{-1}$. Top: time series of PAR data with sinusoidal best fit curve. Second from top: time series of mixed layer depth data with sinusoidal best fit curve. Second from bottom: time series of surface model phytoplankton concentration predictions compared with chlorophyll data. Bottom: time series of surface model phytoplankton and zooplankton predictions.
for the coexisting equilibrium on December 20 but turns directly away from the border immediately afterwards. Under these circumstances, the bloom is expected to occur almost immediately after the winter solstice, which is a manifestation of the attracting/repelling bloom mechanism. This is what happens in the second plot from the bottom of Figure 4.1 as the phytoplankton only equilibrium first attracts and then repels the system.

To make the model phytoplankton bloom occur later in the year, the \(D_{\text{max}}\) versus \(\rho\) trajectory needs to turn away from the border between the domain of stability of the phytoplankton-only equilibrium and the domain of stability of the coexisting equilibrium later than the winter solstice. This borderline can be moved to the right by increasing \(k_W\) or decreasing \(a\) as shown in section 3.3. Figure 4.3 shows the predictions of the system (3.1) in the North Atlantic region using parameter values in Tables 2.1 and 3.1 except that now \(h_{\text{max}} = 0.75 \text{ d}^{-1}\), \(a = 0.5 \text{ (mmol N m}^{-3})^{-1}\) and \(k_W = 0.04 \text{ m}^{-1}\). An increase in \(h_{\text{max}}\) is chosen to prevent an excessive duration of the bloom. It is seen in the second plot from the bottom of Figure 4.3 that the timing of the bloom termination is an improvement from the timing of the bloom termination in Figure 4.1. However, two problems materialize with this change of parameterization. First, there is a late-year decline in the model phytoplankton concentration that is not indicated in the chlorophyll data. Second, the bottom plot of Figure 4.3 shows the zooplankton concentration declining to \(4.1 \times 10^{-4}\) mmol N m\(^{-3}\), an unrealistically low level. These two problems can be explained by the stability diagram in Figure 4.4.

Figure 4.4 shows the stability diagram of system (3.4) using the same parameter values \(h_{\text{max}} = 0.75 \text{ d}^{-1}\), \(a = 0.5 \text{ (mmol N m}^{-3})^{-1}\) and \(k_W = 0.04 \text{ m}^{-1}\) and a trajectory of \(D_{\text{max}}\) versus \(\rho\) based on the sinusoidal approximation of the data from the North Atlantic region. The model phytoplankton bloom occurs well after the winter solstice because the \(D_{\text{max}}\) versus \(\rho\) trajectory moves away from the domain of stability for the phytoplankton-only equilibrium and into the domain of stability for the coexisting equilibrium about half-way between the winter solstice and the vernal equinox. The late year decline in phytoplankton concentration is explained by the \(D_{\text{max}}\) versus \(\rho\) trajectories.
Figure 4.2: Stability diagram for equation system (3.4) with $M = 130$ m, $k_W = 0.02$ m$^{-1}$, $D_{\text{min}} = 10^{-6}$ m$^2$s$^{-1}$, and $h_{\text{max}} = 0.5$ d$^{-1}$. The white (left) region is where the plankton-free equilibrium is stable. The aqua (middle) region is where the phytoplankton-only equilibrium is stable. The yellow (right) region is where the coexisting equilibrium is stable. The dashed curve is the seasonal trajectory of sinusoidal approximations for light response $\rho$ and upper mixed layer diffusion $D_{\text{max}}$ based on the corresponding data from the North Atlantic region 40-45°N, 25-35°W. Four distinct symbols indicate points on the trajectory representing the vernal and autumnal equinoxes and the winter and summer solstices.
Figure 4.3: Time series of solution of system (3.1) with $I(t)$ described by PAR data and $M(t)$ described by mixed layer depth data. All data averaged over the region 40-45°N, 25-35°W in the North Atlantic. Parameter values from Table 2.1 and Table 3.1 except for $k_W = 0.04 \text{ m}^{-1}$, $a = 0.5 \text{ (mmol N m}^{-3})^{-1}$, $D_{\text{min}} = 10^{-6} \text{ m}^2\text{s}^{-1}$, and $h_{\text{max}} = 0.75 \text{ d}^{-1}$. Top: time series of PAR data with sinusoidal best fit curve. Second from top: time series of mixed layer depth data with sinusoidal best fit curve. Second from bottom: time series of surface model phytoplankton concentration predictions compared with chlorophyll data. Bottom: time series of surface model phytoplankton and zooplankton predictions.
trajectory entering the domain of stability of the phytoplankton-only equilibrium and getting close to the domain of stability of the plankton-free equilibrium at the winter solstice. The trajectory entering the domain of stability for the phytoplankton-only equilibrium causes the zooplankton concentration to rapidly decline to unrealistically low levels. Therefore, accurately simulating blooms requires that the $D_{\text{max}}$ versus $\rho$ trajectory must either spend a minimal amount of time in the domain of stability for the phytoplankton-only equilibrium or stay out of it completely.

Although the attracting/repelling bloom mechanism that exists in system (3.1), under forced change in $\rho$ and $M$, partially explains the dynamical causes of phytoplankton blooms in the North Atlantic, the timing of blooms simulated by the system (3.1) is not correct (Figures 4.1 and 4.3). A more accurate estimation of the seasonal changes in diffusion in the upper mixed layer of the ocean could be beneficial. Incorporating ocean temperature data into the phytoplankton growth term, as is done in Kuhn et al. [35], could also affect the linear stability of the system (3.1). Non-dimensionalizing system (3.1) could be useful for simplifying the model and better understanding of the impact of parameter groups and parameter variations (see appendix C).
Figure 4.4: Stability diagram for equation system (3.4) with $M = 130$ m, $k_W = 0.04$ m$^{-1}$, $a = 0.5$ (mmol N m$^{-3}$)$^{-1}$ and $h_{max} = 0.75$ d$^{-1}$. The white (left) region is where the plankton-free equilibrium is stable. The aqua (middle) region is where the phytoplankton-only equilibrium is stable. The yellow (right) region is where the coexisting equilibrium is stable. The dashed curve is the seasonal trajectory of sinusoidal approximations for light response $\rho$ and upper mixed layer diffusion $D_{max}$ based on the corresponding data from the North Atlantic region 40-45°N, 25-35°W. Four distinct symbols indicate points on the trajectory representing the vernal and autumnal equinoxes and the winter and summer solstices.
Chapter 5

CONCLUSIONS

In complex planktonic systems, it is not intuitive what the static plankton states would be if there is no seasonal forcing, or which parameters affect the mathematical attractors that influence the behavior of plankton populations. Light, diffusion, and mixed layer depths have all been suggested as dominant drivers of plankton populations. In this dissertation, we determined the influence of surface light, diffusion strength and mixed layer depth on the stability of the equilibria of an NPZ reaction-diffusion system. We envision our results giving ecologists and modelers theoretical expectations about what state the ecosystem ought to be under certain conditions of light, mixed layer depth and diffusion.

This study of a simple NPZ reaction-diffusion model informs more complex plankton ecology models. Some plankton models have so many state variables or parameters that determining their equilibria and their stability properties can be difficult or impossible. However, we expect models that have similar structure and parameterizations to the model in this dissertation to exhibit similar dynamical behavior. Therefore, we anticipate that the results of this analysis will provide insight into future plankton modelling studies.

Underlying causes of seasonal, marine phytoplankton blooms are a debated subject. The seasonally changing quantities of diffusion and mixed layer depth have assumed roles in phytoplankton bloom theory as critical quantities that either restrict phytoplankton access to light (Critical Depth Hypothesis), limit phytoplankton accumulation (Critical Turbulence Hypothesis) or reduce contact rates between phytoplankton and zooplankton (Dilution-Recoupling Hypothesis). With the understanding of blooms as resulting from a change of which equilibrium is attracting, our results
partially agree with these theories. As discussed in section 1.3, a key assumption of
Sverdrup’s Critical Depth Hypothesis [11] is that the mixed layer be characterized by
high turbulence. Recall from section 3.3 that mixed layer depth has a significant in-
fluence on which equilibrium is attracting only when diffusion is high. However, it
is also shown in section 3.3 that diffusion influences which equilibrium is attracting
regardless of the mixed layer depth. This is in accordance with the Critical Turbulence
Hypothesis. Like the Dilution-Recoupling Hypothesis, the initiation of our “saddle
point bloom” mechanism relies on reduced contact rates between phytoplankton and
zooplankton, although not exclusively as a result of dilution.

Our results mostly support the theory of Behrenfeld and Boss [54], who suggest
the abiotic factors that cause blooms do so by disrupting predator-prey relationships
instead of by controlling growth rates of phytoplankton as theorized by the Critical
Depth Hypothesis and the Critical Turbulence Hypothesis. We suggest that seasonal
changes in solar radiation, diffusion, and, to a lesser degree, mixed layer depth can
cause such a disruption. In this dissertation, we follow up on this notion by iden-
tifying a saddle point bloom mechanism in an ordinary differential equation system
and a similar attracting/repelling mechanism in a reaction diffusion system that can
cause phytoplankton blooms. We propose that phytoplankton blooms are caused by
the temporary attraction of a phytoplankton-only equilibrium state of the planktonic
ecosystem. We then evaluate the predictive power of the attracting/repelling bloom
mechanism by analyzing the effect of seasonal data from solar radiation and mixed
layer depth on the dynamical causes of phytoplankton blooms.

Although our model fails to imitate phytoplankton blooms to the degree of ac-
ccuracy of more complex models, such as that of Kuhn et al. [35], our model provides
informative results. The simplicity of our model allows for the analysis of its dynam-
ics. These dynamical properties also appear to be present in more complex models.
For example, Kuhn et al. [35] used a parameter optimization scheme on an advection-
diffusion-reaction NPZD (Nutrient-Phytoplankton-Zooplankton-Detritus) model to pro-
duce results that mimic phytoplankton blooms in the North Atlantic quite well. Their
results, however, suggest that the dynamical processes described in this dissertation are involved. Before a bloom, as in this dissertation, their phytoplankton levels are low and their zooplankton levels are low but reasonable. This suggests that low sunlight and high diffusive turbulence have pushed the system close to a point where a phytoplankton-only equilibrium is the attracting state. The phytoplankton bloom that follows is likely due to the influence of a phytoplankton-only equilibrium which temporarily attracts and then repels the system.

If it is true that phytoplankton blooms in the North Atlantic are primarily caused by a disruption in the predator-prey balance as suggested by Behrenfeld and Boss [54], this dissertation provides a detailed explanation of the underlying mechanism for phytoplankton bloom formation with reference to attracting and repelling states of the plankton system. We postulate that the disruption in the predator-prey balance suggested by Behrenfeld and Boss [54] is set up by winter conditions rendering a low concentration of phytoplankton and an even lower (but reasonable) concentration of zooplankton. The return of spring conditions (increased sunlight and decreased diffusion) causes the phytoplankton only equilibrium to temporarily attract and then repel the system toward a co-existing equilibrium in late spring. In the fall, the system is disrupted again by decreased light and increased diffusion, allowing for the possibility of the phytoplankton only equilibrium to attract the system in the spring, thus completing the cycle. Although our simple model (3.1) does not capture the secondary details of the bloom process, it can be useful for explaining the mechanics of more complex models and for understanding marine planktonic ecosystems.
BIBLIOGRAPHY


Appendix A

NUMERICAL SCHEME: REACTION-DIFFUSION EQUATIONS

This appendix describes the numerical scheme used in this dissertation for solving the reaction-diffusion NPZ equations (3.1). First, let $u(\xi, t) = (P(\xi, t), Z(\xi, t), N(\xi, t))$. Then we represent the “reaction part” of the reaction-diffusion equation as

$$f(u) = f(P, Z, N) = \begin{pmatrix} \rho e^{-kW} \mu_{\max} \frac{N}{kN + N} P - h_{\max} \left(1 - e^{-aP}\right) Z - m_P P \\ \alpha h_{\max} \left(1 - e^{-aP}\right) Z - m_Z Z \\ -\rho e^{-kW} \mu_{\max} \frac{N}{kN + N} P + (1 - \alpha) h_{\max} \left(1 - e^{-aP}\right) Z + m_P P + m_Z Z \end{pmatrix}. \tag{A.1}$$

With this change of notation, the reaction diffusion system (3.1) can be written as

$$\partial_t u = \partial_\xi (D \partial_\xi u) + f(u). \tag{A.2}$$

Consider the domain $[0, H] \times [0, T]$ where $0 \leq \xi \leq H$ meters and $0 \leq t \leq T$ days. For the water column, let the interval $[0, H]$ be discretized by $m$ nodes, each a distance of $\Delta \xi = \frac{H}{m-1}$ apart. For time, let the interval $[0, T]$ be discretized by $k$ nodes, each a distance of $\Delta t = \frac{T}{k-1}$ apart. For $j = 1, \ldots, m$ and $n = 1, \ldots, k$ we use a Crank-Nicolson [71] scheme to solve system (3.1) as follows:

$$\frac{u_j^{n+1} - u_j^n}{\Delta t} = \frac{1}{2\Delta \xi^2} \left[ D_{j+1/2}^n (u_{j+1}^n - u_j^n) - D_{j-1/2}^n (u_j^n - u_{j-1}^n) \right. \left. + D_{j+1/2}^{n+1} (u_{j+1}^{n+1} - u_j^{n+1}) - D_{j-1/2}^{n+1} (u_j^{n+1} - u_{j-1}^{n+1}) \right] + f(u_j^n). \tag{A.3}$$

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Note that since the diffusion coefficient $D$ is known then we can define $D_{j-1/2}^n$, $D_{j+1/2}^n$, etc. Since this is an implicit scheme, a matrix equation $Ax = b$ is solved with new values of $A$ and $b$ for each state variable ($P, Z, \text{ or } N$) at each time step. Each matrix equation is solved using the GMRES package in MATLAB. Initial conditions for system (3.1) are set to $P(\xi) \equiv 0.2 \text{ mmol N m}^{-3}$, $Z(\xi) \equiv 0.2 \text{ mmol N m}^{-3}$, and $N(\xi) \equiv 1.6 \text{ mmol N m}^{-3}$. These three values were selected by Gentleman and Neuheimer [61] for their ordinary differential equations NPZ model.

The no-flux boundary condition at the surface, $\partial_\xi u(0,t) = 0$, is enforced by using the second-order forward finite difference approximation for the first derivative with respect to $\xi$:

$$\partial_\xi u(\xi,t) \approx \frac{-3u(\xi,t) + 4u(\xi + \Delta\xi,t) - u(\xi + 2\Delta\xi,t)}{2\Delta\xi}.$$  

The no-flux boundary condition at the bottom, $\partial_\xi u(H,t) = 0$, is enforced by using the second-order backward finite difference approximation for the first derivative with respect to $\xi$:

$$\partial_\xi u(\xi,t) \approx \frac{3u(\xi,t) - 4u(\xi - \Delta\xi,t) + u(\xi - 2\Delta\xi,t)}{2\Delta\xi}.$$  

Thus the first row of each matrix $A$ is $[-3 \quad 4 \quad -1 \quad 0 \quad \cdots \quad 0]$, the last row of each matrix is $[0 \quad \cdots \quad 0 \quad 1 \quad -4 \quad 3]$, and the first and last entry of each vector $b$ is 0.

One test of the validity of the scheme (A.3) is whether or not nitrogen is conserved. Solutions to equations (3.1) conserve the total concentration of nitrogen at all depths, $N_T \equiv \frac{1}{H} \int_0^H (P + Z + N)d\xi$, at all times. Conservation of this quantity using the numerical scheme (A.3) can be achieved with $\Delta t = 0.1$ days and $\Delta\xi = 5$ m for $D_{max} = 10^{-3}$ m$^2$s$^{-1}$ or lower. Values of $D_{max}$ greater than $10^{-3}$ m$^2$s$^{-1}$ tend to require smaller values of $\Delta t$ in order to conserve the total nitrogen concentration $N_T$. Consequently, this entails longer running times for the algorithm.

Another way to test the validity of the scheme is to compute a stable equilibrium of the system (3.4) using the methods in section 3.2 and then check if the system
converges to this equilibrium. Figure A.1 shows the results of such a test. Figure A.1a (reproduced from Figure 3.5b) is a stability diagram of system (3.4) with parameter values from Tables 2.1 and 3.1 except that $h_{\text{max}} = 0.5 \text{ day}^{-1}$ and $M = 250 \text{ m}$. Figure A.1b shows a computed phytoplankton-only equilibrium of this system with $\rho = 0.2$ and $D_{\text{max}} = 10^{-3.5} \text{ m}^2\text{s}^{-1}$ (as indicated in the title of the graph). According to Figure A.1a, the phytoplankton-only equilibrium should be stable. Figure A.1c shows the depth profile of the solution of the system with $\rho = 0.2$ and $D_{\text{max}} = 10^{-3.5} \text{ m}^2\text{s}^{-1}$ after 365 days, which matches the predicted equilibrium. Figure A.1d shows a computed coexisting equilibrium of this system with $\rho = 0.6$ and $D_{\text{max}} = 10^{-3} \text{ m}^2\text{s}^{-1}$. According to Figure A.1a, the coexisting equilibrium should be stable. Figure A.1e shows the depth profile of the solution of the system with $\rho = 0.6$ and $D_{\text{max}} = 10^{-3} \text{ m}^2\text{s}^{-1}$ after 365 days, which matches the predicted equilibrium. Figures A.1c and A.1e use initial conditions $P(\xi) \equiv 0.2 \text{ mmol N m}^{-3}$, $Z(\xi) \equiv 0.2 \text{ mmol N m}^{-3}$, and $N(\xi) \equiv 1.6 \text{ mmol N m}^{-3}$ [61]. Not only is the stability of the predicted equilibria confirmed, but the numerical scheme A.3 also converges to the predicted equilibrium.
Figure A.1: Stability test for the numerical scheme (A.3) for the unforced in time system (3.4). (a) Stability diagram reproduced from Figure 3.5b. White (left) region: plankton-free equilibrium is stable, Aqua (middle) region: phytoplankton-only equilibrium is stable, Yellow (right) region: coexisting equilibrium is stable. (b) Computed phytoplankton-only equilibrium for $\rho = 0.2$ and $D_{\text{max}} = 10^{-3.5} \text{m}^2\text{s}^{-1}$. (c) Depth profile of the solution of the system for $\rho = 0.2$ and $D_{\text{max}} = 10^{-3.5} \text{m}^2\text{s}^{-1}$ after 365 days. (d) Computed coexisting equilibrium with $\rho = 0.6$ and $D_{\text{max}} = 10^{-3} \text{m}^2\text{s}^{-1}$. (e) Depth profile of the solution of the system with $\rho = 0.6$ and $D_{\text{max}} = 10^{-3} \text{m}^2\text{s}^{-1}$ after 365 days.
Appendix B

CONSTRUCTION OF REACTION-DIFFUSION JACOBIAN MATRIX

This appendix describes the construction of the Jacobian matrix $J(\tilde{P}, \tilde{Z})$ in equation (3.8). For the discretization of the depth domain $[0, H]$ into $m$ nodes ($\xi_j$ for $j = 1, \ldots, m$), we begin the construction of $J(\tilde{P}, \tilde{Z})$ by writing

$$J(\tilde{P}, \tilde{Z}) = \begin{bmatrix} \frac{\partial F}{\partial P} & \frac{\partial F}{\partial Z} \\ \frac{\partial G}{\partial P} & \frac{\partial G}{\partial Z} \end{bmatrix} + \begin{bmatrix} \frac{\partial}{\partial \xi} \left( \frac{D}{\partial \xi} \right) & 0 \\ 0 & \frac{\partial}{\partial \xi} \left( \frac{D}{\partial \xi} \right) \end{bmatrix}$$

where $J(\tilde{P}, \tilde{Z})$ has $2m \times 2m$ entries and

$$a_{11}^{(j)} = \frac{\partial}{\partial P} F(\tilde{P}(\xi_j), \tilde{Z}(\xi_j)), \quad a_{12}^{(j)} = \frac{\partial}{\partial Z} F(\tilde{P}(\xi_j), \tilde{Z}(\xi_j)),$$

$$a_{21}^{(j)} = \frac{\partial}{\partial P} G(\tilde{P}(\xi_j), \tilde{Z}(\xi_j)), \quad a_{22}^{(j)} = \frac{\partial}{\partial Z} G(\tilde{P}(\xi_j), \tilde{Z}(\xi_j)).$$
For rows $2, \ldots, m-1, m+2, \ldots, 2m-1$, the derivative $\frac{\partial}{\partial \xi}$ is approximated by the second-order centered finite difference approximation
\[
\frac{\partial}{\partial \xi} u(\xi, t) \approx \frac{u(\xi + \Delta \xi, t) - u(\xi - \Delta \xi, t)}{2\Delta \xi}
\]
and the derivative $\frac{\partial^2}{\partial \xi^2}$ is approximated by the second-order centered finite difference approximation
\[
\frac{\partial^2}{\partial \xi^2} u(\xi, t) \approx \frac{u(\xi + \Delta \xi, t) - 2u(\xi, t) + u(\xi - \Delta \xi, t)}{(\Delta \xi)^2}.
\]

For rows 1 and $m+1$, the derivative $\frac{\partial}{\partial \xi}$ is approximated by the second-order forward finite difference approximation
\[
\frac{\partial}{\partial \xi} u(\xi, t) \approx -\frac{3}{2}u(\xi, t) + \frac{4}{2}u(\xi + \Delta \xi, t) - \frac{1}{2}u(\xi + 2\Delta \xi, t).
\] (B.1)
and the derivative $\frac{\partial^2}{\partial \xi^2}$ is approximated by the second-order forward finite difference approximation
\[
\frac{\partial^2}{\partial \xi^2} u(\xi, t) \approx \frac{2u(\xi, t) - 5u(\xi + \Delta \xi, t) + 4(u(\xi + 2\Delta \xi, t) - u(\xi + 3\Delta \xi, t))}{(\Delta \xi)^2}.
\] (B.2)

In rows 1 and $m+1$, no-flux boundary conditions are imposed by setting $\frac{\partial}{\partial \xi} \hat{P} = \frac{\partial}{\partial \xi} \hat{Z} = 0$, which from equation (B.1) implies
\[
-3\hat{P}(\xi_1) + 4\hat{P}(\xi_2) - \hat{P}(\xi_3) = 0 = -3\hat{Z}(\xi_1) + 4\hat{Z}(\xi_2) - \hat{Z}(\xi_3).
\] (B.3)

Consequently, $\hat{P}(\xi_1) = \frac{4}{3}\hat{P}(\xi_2) - \frac{1}{3}\hat{P}(\xi_3)$ and $\hat{Z}(\xi_1) = \frac{4}{3}\hat{Z}(\xi_2) - \frac{1}{3}\hat{Z}(\xi_3)$. Using these substitutions for $\hat{P}(\xi_1)$ and $\hat{Z}(\xi_1)$ we set the first row of $J(\hat{P}, \hat{Z})$ as
\[
\begin{bmatrix}
0 & \left(\frac{4}{3}a_{11}^{(1)} - \frac{7}{3}\Delta \xi^2\right) & \left(\frac{10}{3}\Delta \xi^2 - \frac{1}{3}a_{11}^{(1)}\right) & \frac{D(\xi_1)}{\Delta \xi^2} & 0 & \cdots & 0 & a_{12}^{(1)} & \cdots & 0
\end{bmatrix}
\]
and row $m+1$ as
\[
\begin{bmatrix}
a_{21}^{(1)} & 0 & \cdots & 0 & \left(\frac{4}{3}a_{22}^{(1)} - \frac{7}{3}\Delta \xi^2\right) & \left(\frac{10}{3}\Delta \xi^2 - \frac{1}{3}a_{22}^{(1)}\right) & \frac{D(\xi_1)}{\Delta \xi^2} & 0 & \cdots & 0
\end{bmatrix}.
\]
For rows $m$ and $2m$, the derivative $\frac{\partial}{\partial \xi} u(\xi, t)$ is approximated by the second-order backward finite difference approximation

$$\frac{\partial}{\partial \xi} u(\xi, t) \approx \frac{3u(\xi, t) - 4u(\xi - \Delta\xi, t) + u(\xi - 2\Delta\xi, t)}{2\Delta\xi}. \quad \text{(B.4)}$$

and the derivative $\frac{\partial^2}{\partial \xi^2} u(\xi, t)$ is approximated by the second-order backward finite difference approximation

$$\frac{\partial^2}{\partial \xi^2} u(\xi, t) \approx \frac{2u(\xi, t) - 5u(\xi - \Delta\xi, t) + 4(\xi - 2\Delta\xi, t) - u(\xi - 3\Delta\xi, t)}{(\Delta\xi)^2}. \quad \text{(B.5)}$$

In rows $m$ and $2m$, no-flux boundary conditions are imposed by setting $\frac{\partial}{\partial \xi} \hat{P} = \frac{\partial}{\partial \xi} \hat{Z} = 0$, which from equation (B.4) implies

$$\hat{P}(\xi_{m-2}) - 4\hat{P}(\xi_{m-1}) + 3\hat{P}(\xi_{m}) = 0 = \hat{Z}(\xi_{m-2}) - 4\hat{Z}(\xi_{m-1}) + 3\hat{Z}(\xi_{m}). \quad \text{(B.6)}$$

Consequently, $\hat{P}(\xi_{m}) = \frac{4}{3} \hat{P}(\xi_{m-1}) - \frac{1}{3} \hat{P}(\xi_{m-2})$ and $\hat{Z}(\xi_{m}) = \frac{4}{3} \hat{Z}(\xi_{m-1}) - \frac{1}{3} \hat{Z}(\xi_{m-2})$. Using these substitutions for $\hat{P}(\xi_{m})$ and $\hat{Z}(\xi_{m})$ we set row $m$ of $J(\hat{P}, \hat{Z})$ as

$$\begin{bmatrix}
0 \cdots 0 \\
0 \cdots 0 \\
0 \cdots 0 \\
0 \cdots 0 \\
(\frac{4}{3} a_{11}^{(m)} - \frac{7}{3} a_{12}^{(m)}) \\
0 \cdots 0 \\
\end{bmatrix}$$

and row $2m$ as

$$\begin{bmatrix}
0 \cdots 0 \\
0 \cdots 0 \\
0 \cdots 0 \\
0 \cdots 0 \\
(\frac{4}{3} a_{21}^{(m)} - \frac{7}{3} a_{22}^{(m)}) \\
0 \cdots 0 \\
\end{bmatrix}.$$
Appendix C
NON-DIMENSIONAL MODEL

To aid in our analysis of the effects of the parameters, we rescale equation (3.1) using the substitutions in Table C.1 to obtain a nondimensional set of equations. We choose to scale all rates by $\mu_{max}$ since we expect $\mu_{max}$ to be the largest of the rates. If the maximum grazing rate or the phytoplankton mortality rate were to be larger than the phytoplankton growth rate then the phytoplankton would become extinct and the zooplankton population would follow. We scale the state variables by $N_T$ because $N_T$ is at least as large as any of the state variables. We set nondimensional time and nondimensional depth as $\tau = \mu_{max} t$ and $\omega = k_W \xi$, respectively. Equation (C.1) gives the nondimensional reduced system.

$$\begin{align*}
\partial_\tau p &= \rho e^{-\omega} \frac{1-p-z}{\beta+1-p-z}p - \sigma \left(1 - e^{-\Lambda p}\right)z - \delta p + \partial_\omega (d \partial_\omega p) \\
\partial_\tau z &= \alpha \sigma \left(1 - e^{-\Lambda p}\right)z - \epsilon z + \partial_\omega (d \partial_\omega z)
\end{align*}$$

(C.1)

Table C.1 and equations (C.1) give insight into the effects of changes in parameters on the predictions of the model (3.1). Note that the nondimensional diffusion

<table>
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<tr>
<td>$p = \frac{P}{N_T}$</td>
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<tr>
<td>$z = \frac{Z}{N_T}$</td>
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<tr>
<td>$\rho = \frac{\Gamma I}{\sqrt{\mu_{max}^2 + \Gamma^2 \Gamma^2}}$</td>
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<tr>
<td>$\beta = \frac{k_N}{N_T}$</td>
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<tr>
<td>$\sigma = \frac{h_{max}}{\mu_{max}}$</td>
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<tr>
<td>$\Lambda = a N_T$</td>
</tr>
<tr>
<td>$\delta = \frac{m_P}{\mu_{max}}$</td>
</tr>
<tr>
<td>$\epsilon = \frac{m_Z}{\mu_{max}}$</td>
</tr>
<tr>
<td>$\eta = \frac{m_Z}{\alpha h_{max}}$</td>
</tr>
<tr>
<td>$d = \frac{k_W D}{\mu_{max}}$</td>
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</table>
coefficient \( d \) can be written as \( d = \frac{k_2^2D_{\text{max}}}{\mu_{\text{max}}} \). This indicates the importance of the ratio of the diffusion rate to the phytoplankton growth rate, a ratio that is relevant to the Critical Turbulence Hypothesis. According to this theory, if turbulent mixing is less than a critical turbulence then phytoplankton growth rates exceed the vertical mixing rates and a bloom can develop regardless of the mixed layer depth [10]. This suggests that the ratio \( \frac{k_2^2D_{\text{max}}}{\mu_{\text{max}}} \) ought to be below a certain value for a bloom to be possible. Although Huisman et al. [10] did not find an analytical expression for critical turbulence, they defined the conditions for phytoplankton bloom development as the conditions that can “support a positive steady-state population.” The saddle point bloom mechanism described in this dissertation works when the coexisting equilibrium is stable. Perhaps a maximum value of \( \frac{k_2^2D_{\text{max}}}{\mu_{\text{max}}} \) can be found computationally for the coexisting equilibrium to be stable. This may determine a necessary condition for blooms to occur.

We can write the thresholds \( \bar{P}_E \) (minimum value of \( \rho \) for which the phytoplankton-only equilibrium exists) and \( \bar{P}_S \) (minimum value of \( \rho \) for which the phytoplankton-only equilibrium is stable) from chapter 2 in terms of nondimensional parameters from Table C.1:

\[
\bar{P}_E = \delta (\beta + 1), \quad \bar{P}_S = \delta \left[ 1 + \frac{\beta}{1 + \frac{1}{\Lambda} \ln \left( 1 - \eta \right)} \right]. \tag{C.2}
\]

Several nondimensional parameters influence the stability properties of the ordinary differential equation system (2.3). Both \( \bar{P}_E \) and \( \bar{P}_S \) increase with \( \delta \) (the ratio of the phytoplankton mortality rate to maximum phytoplankton growth rate) and \( \beta \) (the ratio of the half-saturation constant to the total nutrient concentration). However, \( \bar{P}_S \) depends on the parameters \( \Lambda \) (product of Ivlev decay constant and total nutrient concentration) and \( \eta \) (ratio of zooplankton mortality rate to maximum zooplankton growth rate) whereas \( \bar{P}_E \) does not. \( \bar{P}_S \) decreases with \( \Lambda \) and increases with \( \eta \). Thus, for example, a decrease in \( \eta \) would narrow the interval of stability \((\bar{P}_E, \bar{P}_S)\) of the phytoplankton-only equilibrium whereas an increase in \( \eta \) would widen the interval.
## Appendix D

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