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Nonlinear Models of Zooplankton Communities

A thesis submitted in partial fulfillment of the requirement
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Abstract

Modeling zooplankton dynamics accurately is increasingly important because zoo-plankton can have a critical impact on several environmental issues ranging from eutrophication to climate change. Because of the importance of zooplankton in marine ecosystems, there is a need to develop precise mathematical models. Most models, however, set zooplankton mortality as due to predation only. This approach is inaccurate as many zooplankton can die from non-predatory causes such as disease or starvation. Here we construct a model that includes both predatory and non-predatory zooplankton mortality rather than a linear differential equation model that relies on curve-fitting to data. Through MATLAB simulations, this theoretical nonlinear model was found to be a strongly contracting system even under certain amounts of stochastic influence. While a linear approach when modeling marine species is the natural first step, a nonlinear approach, which is based more on mathematical and ecological theories rather than curve-fitting, allows for more complicated and realistic dynamics in addition to more accurate predictions.

Contents

List of Figures

Chapter 1

Introduction

Accurate predictions of zooplankton abundances are important for modeling populations in marine food webs. Zooplankton play a critical role in aquatic ecosystems, as they are the main grazers of phytoplankton and play a key role in recycling materials. Zooplankton are also the primary food source for several species higher in the food web and are therefore considered an indicator species [10]. Any significant decline in zooplankton populations could negatively impact other species including endangered ones. As zooplankton are among the most abundant creatures in the ocean and can easily absorb carbon, they play a large role in the carbon cycle and can impact climate change. In addition, zooplankton grazing has a major impact on other important ecological processes such as eutrophication. Because zooplankton play a critical role in marine ecosystems, it is essential to be able to describe their dynamics with accurate mathematical models.

While zooplankton egg production and development rates have been well studied in the lab, zooplankton mortality rates are difficult to measure. Both predatory and non-predatory mortality rates remain the least studied processes [7]. Current models, such as the one published by Elliott and Tang in 2011 [7], simply set the mortality rates as constants or linear functions of temperature, which is often not biologically realistic as the mortality rate can reach zero at low temperatures. While knowledge of mortality rates in zooplankton populations is incomplete, mortality rates are one of the most critical aspects of an accurate zooplankton model. Many models use the mortality rate as a closure term that is fine-tuned to the model to ensure stability and accuracy [14].

In a paper [9] recently published in the 2013 Conference Proceedings on BEER, Professor Day, Professor LaMar, Kate Shipman and I studied Elliott and Tang's [7] linear population model of *Acartia tonsa*, the dominant species of zooplankton in the Chesapeake Bay. We built a lower-dimensional model by condensing stage classes with similar life history traits. This lower-dimensional model showed similar

results to the higher-dimensional Elliott and Tang model in both sensitivity and parameter shift analyses. Because a model with fewer dimensions is more tractable, this result indicates that condensed models can be used in future analyses.

In addition, we also studied the effects of the mortality rates (both predatory and non-predatory) in both the original and condensed models. Recent field studies have shown that dead zooplankton are a large proportion of total zooplankton biomass, on average 30% in the Chesapeake Bay [7]. This result reveals that dead zooplankton may be mistakenly counted as live zooplankton, and it also indicates that a large portion of zooplankton can die from non-predatory causes because their bodies are found in the water column still intact. Non-predatory causes of death for zooplankton include starvation, injury, diseases, parasites, and other environmental stressors [7]. This improvement in the differentiation between live and dead zooplankton in samples can be used to improve estimates of predatory and non-predatory mortality rates. In our paper, we showed that both models are highly sensitive to error in the mortality terms, suggesting that further study and data collection into the mortality rates can greatly improve model accuracy.

Not only do a large percentage of zooplankton die from non-predatory causes, but in many zooplankton species, including the dominant species *Acartia tonsa* in the Chesapeake Bay, cannibalism and intra-specific competition are the predominant forms of predation [13, 14]. While cannibalism may appear to be a counterproductive way of feeding, it can stabilize population systems. Young individuals who escape cannibalism have fewer competitors, and the population of zooplankton might not fluctuate as much and might depend less on the frequency of phytoplankton blooms [4].

Because of the prevalence of non-predatory mortality, predatory mortality, and cannibalism in the *Acartia tonsa* zooplankton, a nonlinear mathematical model that separates these different types of mortality may be the best approach. In addition, because we found that a lower-dimensional model shows similar results to a higher-dimensional model, a low-dimensional model will be used. In Chapter 2 we will give an overview of how we build our zooplankton model. Chapter 3 describes the analysis of our model using varying levels of stochasticity. In Chapter 4 we discuss our results and briefly mention future research directions for this project. The MATLAB files used for this project can be found in an online appendix [1].

Chapter 2

Phytoplankton-Zooplankton Model

Because zooplankton abundances depend so heavily on phytoplankton, it is useful to look at zooplankton populations through predator-prey interactions in which zooplankton are the predators and phytoplankton are the prey.

2.1 Basic P-Z Model

The Rosenzweig–MacArthur model [15], developed in 1963, is a commonly used predator-prey model with Holling Type II predation. The Scheffer model [16], developed in 1997, is a modified version of the Rosenzweig–MacArthur that is specific to zooplankton and phytoplankton communities and includes Holling Type III predation on zooplankton by higher trophic level fish. Using standard modeling terms, we constructed the following phytoplankton-zooplankton model based on these two classic predator-prey models to better understand nonlinear effects. The first equation represents the rate of change of phytoplankton while the second one represents the rate of change of zooplankton:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right) - g\frac{P}{\mu + P}Z \tag{2.1a}$$

$$\frac{dZ}{dt} = bg\frac{P}{\mu + P}Z - mZ - \gamma\frac{Z^2}{k^2 + Z^2}. \tag{2.1b}$$

The state variables are:
$P(t)$: the abundance of phytoplankton at time t (days),
$Z(t)$: the abundance of zooplankton at time t (days),
$T(t)$: the water temperature in the Chesapeake Bay at time t (days).

4

The rates are defined as:

Rates	Definition
$r(T)$	phytoplankton growth rate
$K(T)$	phytoplankton carrying capacity
g	maximal zooplankton grazing rate
μ	half-max constant for zooplankton grazing
b	proportion of grazing to growth
$m(T)$	zooplankton non-predatory mortality
$\gamma(T)$	maximal higher trophic grazing rate
k	half-max constant for higher trophic grazing

In our basic P-Z model, the rates r, K, m, and γ are all increasing functions of temperature T. Because some of the rates are functions of temperature, which in turn is a function of time, this model is a non-autonomous system of nonlinear differential equations. The half-max constant μ indicates the density of phytoplankton present in the water column when the zooplankton predation rate is at half of its maximum. The half-max constant k indicates the density of zooplankton present in the water column when the higher trophic fish predation rate is half of its maximum. The values for the rates and constants used in this model are in Appendix A.3.

The temperature function in the model is given by the following expression:

$$T = 16.133 - 11.132 \cdot \cos(2\pi \cdot (t + 28.076)/365), \tag{2.2}$$

where t is time in days [7]. Figure 2.1 contains a plot of the temperature function.

The first term in the phytoplankton differential equation (2.1a) is a logistic growth term for the phytoplankton. Logistic growth is an S-shaped growth pattern in which the growth of the population slows as the population approaches the carrying capacity, K. The negative term is the predation term on phytoplankton with a Holling Type II functional response to predation by zooplankton. The first term in the zooplankton differential equation (2.1b) is the Holling Type II response to predation on phytoplankton with a constant b that indicates how much of the phytoplankton consumed actually goes towards growth in the population. The non-predatory mortality rate (due to disease, starvation, injury etc.) is a linear function of temperature, and finally the predation on zooplankton by higher trophic grazing fish is a Holling Type III functional response.

According to theoretical ecologist Peter Turchin [17], if a predator is a "specialist" and feeds on only one type of food, they are more likely to exhibit a Holling Type II (or hyperbolic) functional response. A Type II functional response indi-
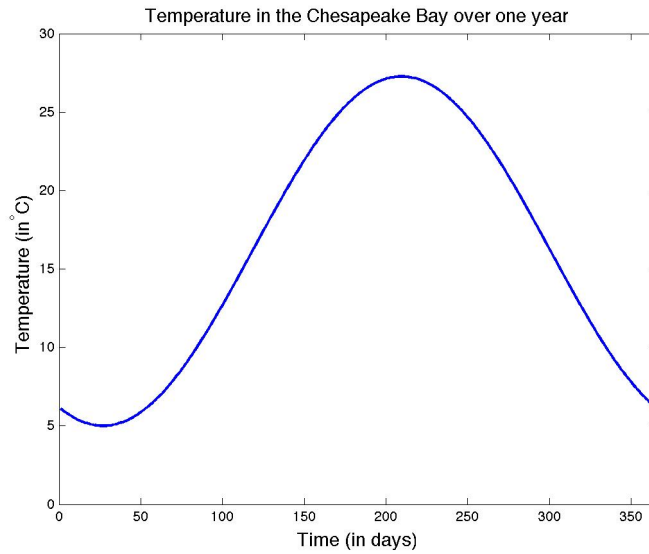
Figure 2.1: *Deterministic surface water temperature in the Chesapeake Bay over the course of one year given by [7].*

cates a decelerating consumption rate as the prey density increases, suggesting that the predator has a limited capacity to process food. If a predator has more than one option for food, a "generalist," they are more likely to exhibit a Holling Type III (or sigmoidal) functional response [17]. This distinction between predator types can be attributed to the functional form of the Type III response curve. The Type III curve has the consumption rate as very low for a low density of prey, but when the density gets high enough, the consumption rate jumps up sharply. This S-shaped curve allows for prey-switching behavior. When the density of the prey is low, a "generalist" predator or consumer does not need to put in the effort to find that prey, as it can consume other species of organisms. The Holling Type II equation does not have this behavior and instead saturates to a maximum consumption rate. In the basic P-Z model without cannibalism (2.1), it is assumed that the zooplankton are "specialists" and only eat phytoplankton, while the higher trophic level fish are "generalists" as they can eat zooplankton among many other prey.

2.2 P-Z Model with Cannibalism

Because a significant portion of zooplankton mortality can be attributed to intra-guild predation, including in the *Acartia tonsa* species [13], a modified version of the basic P-Z model (2.1) is more useful to analyze. The following model is

modified to include intra-guild predation (cannibalism):

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right) - g\frac{c_p P^2}{\mu^2 + c_p P^2 + c_z Z^2}Z \tag{2.3a}$$

$$\frac{dZ}{dt} = bg\frac{c_p P^2 + c_z Z^2}{\mu^2 + c_p P^2 + c_z Z^2}Z - g\frac{c_z Z^2}{\mu^2 + c_p P^2 + c_z Z^2}Z - mZ$$
$$-\gamma\frac{Z^2}{k^2 + Z^2}. \tag{2.3b}$$

The rates and constants for this model are similar to those in the previous model (2.1). The constant c_p indicates the relative preference zooplankton have for eating phytoplankton, while c_z indicates the relative preference zooplankton have for eating other zooplankton. Because the prey choice constants are relative preferences, $c_p + c_z = 1$. Due to the chosen functional form of the predation on phytoplankton and the cannibalism on other zooplankton, this model does not reduce to the basic P-Z model (2.1) when $c_p = 1$ and $c_z = 0$.

One hypothesis, and the one we will adopt in what follows, is that c_p and c_z are constant or close to constant and independent of any other factors, including the relative abundances of phytoplankton and zooplankton or the water temperature. Another reasonable hypothesis is that c_p and c_z depend on the relative abundances of zooplankton, Z, and phytoplankton, P, in the water column, with the prey choice rates taking the functional form:

$$c_z(P, Z) = \frac{1}{1 + \left(aP/Z\right)^2}. \tag{2.4}$$

A third hypothesis is that there is some threshold of phytoplankton, P_0, that will cause the relative prey choice rates to change:

$$c_z(P) = e^{-(P/P_0)^2}. \tag{2.5}$$

For simplicity, the constant prey choice will be used for the rest of the analysis. These choice functions indicate the innate preference zooplankton have for one type of food over another if given the choice between the two. It does not mean that if c_z is high the zooplankton will always eat zooplankton, just that they prefer them if given the choice.

The negative term in the phytoplankton differential equation in the P-Z model with cannibalism (2.3a) is the predation term on phytoplankton with a Holling Type III functional response. The amount of phytoplankton eaten will depend on the preference that zooplankton have for phytoplankton (c_p), the available phytoplankton, and the number of zooplankton in the system. A Holling Type III

response is used because the zooplankton in this model have two choices for prey, and so they are "generalists" and engage in prey-switching behavior [17].

The positive term in the zooplankton differential equation in the P-Z model with cannibalism (2.3b) is the amount of growth zooplankton attain from eating both phytoplankton and other zooplankton. Again, this term is modeled using a Holling Type III functional response. There is also a negative term indicating the predation on zooplankton by other zooplankton. The non-predatory mortality rate and the Holling Type III predation on zooplankton by higher trophic fish are the same as in the previous model without cannibalism (2.1).

The first step in the analysis of the P-Z model is to find the fixed points. To find the fixed points we require $\frac{dZ}{dt} = \frac{dP}{dt} = 0$. Unfortunately, the fixed points in this system cannot be solved by hand. Using the right-hand side of 2.3b, the equation $\frac{dZ}{dt} = 0$ yields a degree five polynomial in Z and cannot be solved on MATLAB. The next step is to nondimensionalize the model in order to simplify the model.

2.2.1 Nondimensionalization of P-Z Model

Nondimensionalization is the process of removing some of the rates and constants in a model by an appropriate substitution of the state variables in order to simplify the equations and make all the rates unitless. Nondimensionalizing the P-Z model with cannibalism (2.3) may make it easier to analyze the dynamics of the model.

To nondimensionalize the P-Z model with cannibalism, let $P = \alpha\tilde{P}$, $Z = \beta\tilde{Z}$, and $t = \tau\tilde{t}$. Then $d\tilde{P} = \frac{1}{\alpha}dP$, $d\tilde{Z} = \frac{1}{\beta}dZ$, and $d\tilde{t} = \frac{1}{\tau}dt$. Let $\tau = \frac{1}{r}$, $\alpha = K$, and $\beta = K$ and choose nondimensionalized functions of temperature $f = \frac{g}{r}$, $h^2 = \frac{\mu^2}{K^2}$, $j = \frac{m}{r}$, $l = \frac{\gamma}{rK}$, and $q^2 = \frac{k^2}{K^2}$.

Then the nondimensionalized version of the P-Z model is

$$\frac{d\tilde{P}}{d\tilde{t}} = \tilde{P}(1 - \tilde{P}) - c_p f \frac{\tilde{P}^2\tilde{Z}}{h + c_p\tilde{P}^2 + c_z\tilde{Z}^2} \tag{2.6a}$$

$$\frac{d\tilde{Z}}{d\tilde{t}} = bf\tilde{Z}\left(\frac{c_p\tilde{P}^2 + c_z\tilde{Z}^2}{h^2 + c_p\tilde{P}^2 + c_z\tilde{Z}^2}\right) - f\tilde{Z}\left(\frac{c_z\tilde{Z}^2}{h^2 + c_p\tilde{P}^2 + c_z\tilde{Z}^2}\right) \tag{2.6b}$$
$$ - j\tilde{Z} - l\left(\frac{\tilde{Z}^2}{q^2 + \tilde{Z}^2}\right).$$

The constant prey choices would remain the same, as they are already unitless. However, the hypothesis in which the prey choices are functions of P and Z would need to be nondimensionalized as well:

$$c_z(\tilde{P}, \tilde{Z}) = \frac{1}{1 + \left(a\tilde{P}/\tilde{Z}\right)^2}.$$

For the third hypothesis, let $\tilde{P}_0 = \frac{P_0}{K}$. Then the nondimensionalization for the prey choice function in which c_z and c_p depend on a threshold of phytoplankton being reached is

$$c_z(\tilde{P}) = e^{-(\tilde{P}/\tilde{P}_0)^2}.$$

In this model, f, h, j, l, and q are introduced as unitless functions and $\tilde{P}$, $\tilde{Z}$, and $\tilde{t}$ are the modified state variables (see Appendix B.1 for more details on nondimensionalization).

2.2.2   P-Z Model Simulation

The next natural step is to run a simulation of the P-Z model with cannibalism and compare it with existing data to test its accuracy. The MATLAB code titled `PZ_matlab_par.m` [1] plots the temperature in the Chesapeake Bay over one year given by (2.2) from Elliott and Tang [7]. The code also plots the biomass of phytoplankton and zooplankton over the course of a year. The phytoplankton and zooplankton data were collected in terms of individuals in [7] and `http://www.chesapeakebay.net/data`, and these individuals were converted to biomass using [8] to be consistent with the rates and constants we found for our model (see Appendix A.1 and A.2 for the full data set used). This code also gives us the initial and final biomass of phytoplankton and zooplankton, and it will be used when making time-t plots (see Section 3.5.2).

The MATLAB code titled `PZ_matlab2_par.m` [1] uses the same temperature function by Elliott and Tang [7], but adds a higher frequency cosine function to account for the variation in temperature over the course of one day. The amplitude of this higher frequency cosine function is 3°C, an estimate of the natural daily water temperature fluctuations [3]. The new temperature function is given by

$$T = 16.133 - 11.132 \cdot \cos(2\pi \cdot (t + 28.076)/365) - 3 \cdot \sin(2\pi \cdot t). \tag{2.7}$$

This simulation behaves similarly to the one without the added higher frequency cosine function (see Figure 2.2). Additionally, both simulations accurately predict the peaks and the correct order of magnitude of both the phytoplankton and the zooplankton biomass in the Chesapeake Bay. The difference in the order of magnitude biomass between the two species is also captured by the model. The phytoplankton peak around 10 mg/L while the zooplankton peak around 0.02
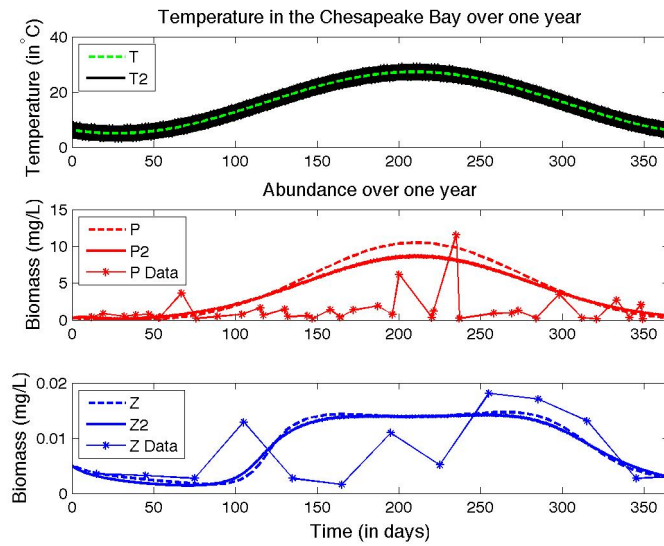
Figure 2.2: *P-Z model (2.3) run over the course of one year with initial conditions $[P, Z] = [0.25, 0.005]$ mg/L. The T, P, and Z refer to the temperature, phytoplankton biomass, and zooplankton biomass when the simulation is run using the regular temperature function (2.2), while T2, P2, and Z2 refer to the simulation using the higher frequency cosine function as the temperature function (2.7). The simulations are plotted against Chesapeake Bay Data (see Appendix A.1 and A.2).*

mg/L, and it is critical that the model can account for such a large difference.

2.3 P-Z-Z Model with Cannibalism and Stage Structure

Because zooplankton tend to eat other zooplankton that are smaller than themselves, introducing stage classes into the cannibalism model would allow us to track cannibalism on a finer scale. In this model, there is a differential equation for the abundance of phytoplankton, one for the abundance of immature zooplankton (Z_0), and one for the abundance of mature zooplankton (Z_1) that can eat the immature zooplankton:

$$\frac{dP}{dt} = rP\Big(1 - \frac{P}{K}\Big) - g\frac{P}{\mu + P}Z_0 - g\frac{c_p P^2}{\mu^2 + c_p P^2 + c_z Z_0^2}Z_1 \qquad (2.8a)$$

$$\frac{dZ_0}{dt} = g\frac{bc_p P^2 + (b-1)c_z Z_0^2}{\mu^2 + c_p P^2 + c_z Z_0^2}Z_1 - dg\frac{P}{\mu + P}Z_0 - m_0 Z_0 \qquad (2.8b)$$

$$-\gamma\frac{Z_0^2}{k^2 + Z_0^2 + Z_1^2}$$

$$\frac{dZ_1}{dt} = dg\frac{P}{\mu + P}Z_0 - m_1 Z_1 - \gamma\frac{Z_1^2}{k^2 + Z_0^2 + Z_1^2}. \qquad (2.8c)$$

The rates and constants in this model are the same as in the P-Z model with cannibalism (2.3) with a couple of new additions. The new parameter, d, is a unitless constant that indicates the proportion of immature zooplankton that develop to the mature zooplankton class. The mortality rate for the immature zooplankton class is given by m_0, while the mortality rate for the mature zooplankton class is given by m_1. It is important to note that the predation by higher trophic level fish, γ, is the same rate for both stage classes. This assumption is a simplification in order to reduce the number of parameters in the model. However, it may not be the case that the predation rates on the different stage classes are the same.

In the phytoplankton differential equation (2.8a), the first term is the logistic growth of the phytoplankton. The second term is predation on phytoplankton by the immature class. This predation term is a Holling Type II functional response, as the immature class can only feed on phytoplankton and are therefore "specialists." The final term in the phytoplankton equation is the predation on phytoplankton by the mature class. This predation term is a Holling Type III functional response, as the mature class are "generalists" [17].

In the immature zooplankton differential equation (2.8b), the first part of the first term indicates the growth in the immature stage class from eating phytoplankton. The $(b-1)$ multiplier in the first term can be further broken down. The role of the constant b indicates the Holling Type III predation of the mature class on the immature class and the percentage of that predation that goes to birth of Z_0. The -1 term indicates the loss of immature zooplankton that are eaten by the mature zooplankton. The second term in the Z_0 term is the development rate to the next stage class as a function of predation on phytoplankton. The third term is the mortality of the immature zooplankton, and the final term is Holling Type III predation by fish on the immature zooplankton.

In the mature zooplankton differential equation (2.8c), the first term indicates the development from the previous stage class. The second term is the mortality rate of the mature zooplankton, and the final term indicates the loss of mature

zooplankton from predation from higher trophic level fish.

2.3.1   Nondimensionalization of P-Z-Z Model

To nondimensionalize the P-Z-Z model with cannibalism, let $P = \alpha\tilde{P}$, $Z_0 = \beta\tilde{Z}_0$, $Z_1 = \Omega\tilde{Z}_1$, and $t = \tau\tilde{t}$. Then $d\tilde{P} = \frac{1}{\alpha}dP$, $d\tilde{Z}_0 = \frac{1}{\beta}dZ_0$, $d\tilde{Z}_1 = \frac{1}{\Omega}$, and $d\tilde{t} = \frac{1}{\tau}dt$. Let $\tau = \frac{1}{r}$, $\alpha = K$, $\beta = K$, $\Omega = K$, and choose nondimensionalized functions of temperature $f = \frac{g}{r}$, $h^2 = \frac{\mu^2}{K^2}$, $j = \frac{m}{r}$, $l = \frac{\gamma}{rK}$, and $q^2 = \frac{k^2}{K^2}$.

Then the nondimensionalized version of (2.8) is

$$
\begin{aligned}
\frac{d\tilde{P}}{d\tilde{t}} &= \tilde{P}(1 - \tilde{P}) - f\tilde{Z}_0\frac{\tilde{P}}{h + \tilde{P}} - f\tilde{Z}_1\frac{c_p\tilde{P}^2}{h^2 + c_p\tilde{P}^2 + c_z\tilde{Z}_0^2} \\
\frac{d\tilde{Z}_0}{d\tilde{t}} &= f\tilde{Z}_1\frac{b_c p\tilde{P}^2 + (b-1)c_z\tilde{Z}_0^2}{h^2 + c_p\tilde{P}^2 + c_z\tilde{Z}_0^2} - df\tilde{Z}_0\frac{\tilde{P}}{h + \tilde{P}} - j\tilde{Z}_0 \\
&\quad -l\frac{\tilde{Z}_0^2}{q^2 + \tilde{Z}_0^2 + \tilde{Z}_1^2} \\
\frac{d\tilde{Z}_1}{d\tilde{t}} &= df\frac{\tilde{P}}{h + \tilde{P}}\tilde{Z}_0 - j\tilde{Z}_1 - l\frac{\tilde{Z}_1^2}{q^2 + \tilde{Z}_0^2 + \tilde{Z}_1^2}.
\end{aligned} \tag{2.9}
$$

In this model, f, h, j, l, and q are introduced as unitless functions and $\tilde{P}$, $\tilde{Z}_0$, $\tilde{Z}_1$, and $\tilde{t}$ are the modified state variables (see Appendix B.2 for more details on nondimensionalization.)

2.3.2   P-Z-Z Model Simulation

The next step is to simulate the P-Z-Z model with cannibalism and compare it to existing data. The MATLAB code titled `PZZ_matlab_par.m` [1] plots the temperature in the Chesapeake Bay over one year given by the function in (2.2). It also plots the biomass of phytoplankton, immature zooplankton, and mature zooplankton over the course of a year (see Figure 2.3). This code gives us the initial and final biomass of phytoplankton and zooplankton, and it can be used when making time-t plots (see Section 3.5.2).
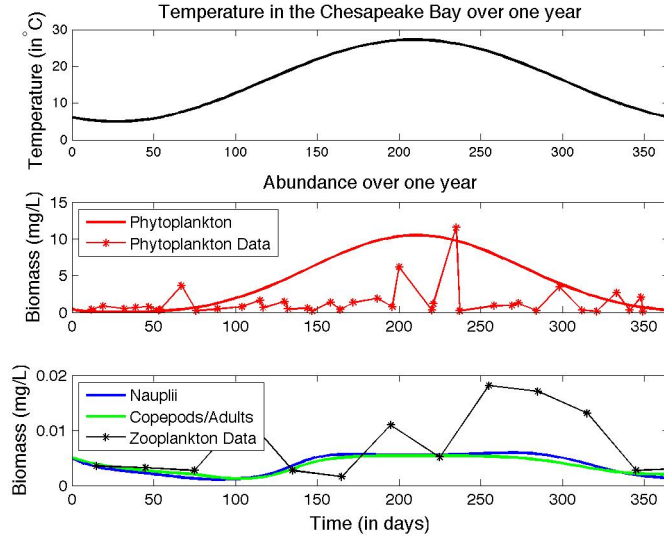
Figure 2.3: *P-Z-Z model (2.8) run over the course of one year with initial conditions* $[P, Z_0, Z_1] = [0.5, 0.005, 0.005]$ *mg/L and temperature function (2.2). Plotted against Chesapeake Bay Data (see Appendix A.1 and A.2).*

2.4   Generalization of the P-Z-Z Model

While the P-Z-Z model is useful, it may be necessary to expand it to include more than just two stage classes for zooplankton. For example, there are thirteen stage classes in the Elliott and Tang linear zooplankton model [7]. While thirteen may be too many to work with, biologists do observe different mortality and development rates depending on the age of the zooplankton. The following is a generalization of the P-Z-Z model that allows for as many as n zooplankton stage classes. It assumes that all the stage classes eat phytoplankton and can eat zooplankton from their own stage class or from lower stage classes. In case the zooplankton do not eat certain stage classes for whatever reason, one can set some of these prey choice constants to 0.

We will use the following nested functional notation to indicate the level of predation or cannibalism from class Z_j onto class X, which can either be phytoplankton (P) or another zooplankton class (Z_i):

$$\chi(X, Z_j) = g \frac{c_{x,z_j} X^2}{\mu^2 + c_{p,z_j} P^2 + \sum_{i=0}^{j} c_{z_i,z_j} Z_i^2} Z_j. \qquad (2.10)$$

We will use the following nested functional notation to indicate the level of preda-

tion from higher trophic levels on a zooplankton class Z_j:

$$\Psi(Z_j) = \gamma_j \frac{Z_j^2}{k^2 + \sum\limits_{i=0}^{n} Z_i^2}. \tag{2.11}$$

We will use the following nested functional notation to indicate the rate of development out of stage class Z_j:

$$\Delta(Z_j) = \delta_j d_j g \frac{c_{p,z_j} P^2 + \sum\limits_{i=0}^{j-1} c_{z_1,z_j} Z_i^2}{\mu^2 + c_{p,z_j} P^2 + \sum\limits_{i=0}^{j} c_{z_i,z_j} Z_i^2} Z_j. \tag{2.12}$$

Using these nested functions, we can generalize the P-Z-Z model as such

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right) - \sum_{i=0}^{n} \chi(P, Z_i) \tag{2.13a}$$

$$\frac{dZ_0}{dt} = bg \frac{c_{p,z_n} P^2 + \sum\limits_{i=0}^{n} c_{z_i,z_n} Z_i^2}{\mu^2 + c_{p,z_n} P^2 + \sum\limits_{i=0}^{n} c_{z_i,z_n} Z_i^2} Z_n - \sum_{i=0}^{n} \chi(Z_0, Z_i) \tag{2.13b}$$

$$\qquad - \Psi(Z_0) - d_0 Z_0 - m_0 Z_0$$

$$\frac{dZ_1}{dt} = d_0 Z_0 - \Delta(Z_1) - \sum_{i=1}^{n} \chi(Z_1, Z_i) - \Psi(Z_1) - m_1 Z_1 \tag{2.13c}$$

$$\qquad\vdots$$

$$\frac{dZ_{n-1}}{dt} = \Delta(Z_{n-2}) - \Delta(Z_{n-1}) - \sum_{i=n-1}^{n} \chi(Z_{n-1}, Z_i) \tag{2.13d}$$

$$\qquad - \Psi(Z_{n-1}) - m_{n-1} Z_{n-1}$$

$$\frac{dZ_n}{dt} = \Delta(Z_{n-1}) - \Psi(Z_n) - m_n Z_n. \tag{2.13e}$$

The rates and constants are all the same as those used in the P-Z and P-Z-Z models except for the subscripts on the prey choices, c. In the simpler models, c_p and c_z indicate the relative preference the zooplankton have for phytoplankton and other zooplankton respectively, with $c_p + c_z = 1$. In this case, however, the different stage classes have different food options from each other. Therefore, there needs to be some differentiation between the prey choice constants depending on the stage class. The first subscript of the c parameter is for the prey choice, while the second

is the predator that is choosing that prey. For example, c_{p,z_1} means the preference stage class Z_1 has for eating phytoplankton, while c_{z_0,z_1} means the preference that stage class Z_1 has for eating zooplankton of stage class Z_0, and so on. The sum of the preferences for each stage class must sum to one:

$$c_{p,z_i} + \sum_{j=i}^{n} c_{z_j,z_i} = 1 \text{ for all } i = 1, \ldots, n. \qquad (2.14)$$

The δ terms are unitless parameters that indicate what percentage of the development term actually progress to the next stage class. It is similar to an efficiency term for the zooplankton: some energy will go to maintenance while some will go to development. All the prey choice constants, mortality rates (m), predation by fish rates (γ), development rates (d), and delta terms (δ) depend on the stage class and therefore have subscripts as well. This generalized equation is allowing for the parameters to be as general as possible, but that does not necessarily mean that these rates are all different from each other in reality.

The first equation, P (2.13a), is the abundance of phytoplankton. The first term is logistic growth, while the following terms are all negative and represent Holling Type III predation from all the stages of zooplankton. The second equation, Z_0 (2.13b), is the abundance of zooplankton eggs. The third and fourth equations, Z_1 to Z_{n-1} (2.13c-2.13d), represent the abundance of the immature, non-reproducing zooplankton stage classes. The final equation, Z_n (2.13e), represents the abundance of the mature stage class.

2.5 Important Dynamical Questions

There are a few biological questions that we want to consider when studying the dynamics of these phytoplankton-zooplankton systems:

- *Mortality* - We have seen in other models that mortality is one of the most important parameters [7]. How can we better represent predatory mortality, non-predatory mortality, and cannibalism in models?

- *Exogenous factors* - What are the effects of external forces such as environmental variability, seasonal temperature forcing, and climate change on the dynamics of these ecosystems? Will adding in stochastic effects significantly change the dynamics of marine ecosystems?

- *Stage structure* - What effect does adding more stage classes have on the dynamics of the zooplankton populations? Does this stabilize the model?

Does the increase in the accuracy of the model offset the decrease in its tractability?

What effect will these factors have on the dynamics of the system? We can use time-t maps with stochastic effects to analyze the dynamics of the models described in this section.

Chapter 3

Stochastic Differential Equations

A **stochastic differential equation** (SDE) is a differential equation that contains at least one stochastic term and leads to a solution that is a stochastic process. We can use stochastic differential equations when modeling random fluctuations in nature. More specifically, we want to use SDEs to model the population dynamics in the presence of stochastic variations in temperature. We will also discretize time by considering a time-t map.

A **time-t map** for the P-Z model maps the initial biomass of phytoplankton and zooplankton to the biomass of phytoplankton and zooplankton that the model predicts will exist after a year. Simulations for the P-Z model with cannibalism (2.3) suggest that there is a fixed point at $(P, Z) = (0.2844, 0.0029)$ mg/L that is globally attracting on the domain $\{(P, Z) \,|\, P, Z > 0\}$. While it is not mathematically very interesting that most of the initial conditions map to the same final abundance of phytoplankton and zooplankton, it is an ecologically good sign that the phytoplankton-zooplankton system is likely stable.

However, in the deterministic model temperature follows a cosine curve. It is unlikely that the actual water temperature will follow this curve precisely and often environmental conditions will fluctuate. One biologically appropriate way to model environmental stochasticity is to add in random fluctuations to the temperature curve because temperature varies on a day-to-day basis. Because many of the rates in the model depend on temperature, if the temperature is randomly varied, other aspects of the model will be influenced as well. One way to add in this stochasticity is to use stochastic differential equations.

More precisely, an SDE is a differential equation with either additive or multiplicative noise terms. Adding a random noise term, $N(t)$, we can model stochasticity in a simple exponential growth differential equation as

$$dX(t) = rX(t) \cdot dt + N(t) \cdot dt. \tag{3.1}$$

Another way to add noise to this differential equation would be to modify the growth rate r:

$$
\begin{aligned}
dX(t) &= \big(r + N(t)\big)X(t) \cdot dt \\
&= rX(t) \cdot dt + N(t)X(t) \cdot dt.
\end{aligned}
\tag{3.2}
$$

Both additive and multiplicative versions of adding noise are valid. It is up to the modeler to decide which version is easier to use or more accurately represents the state variable in question. The stochastic term can be added on the end, to the growth rate r, or, in more complicated models, to other parameters such as the carrying capacity, K. How stochasticity is added is a modeling issue [2, 6, 12].

3.1 The Wiener Process

One of the most commonly used continuous-time stochastic processes that further explains the noise term $N(t)$ is called the Wiener process [12], also known as standard Brownian motion. The Wiener process represents a continuous-time random walk. It is (*almost surely*) continuous everywhere in t, though it is not differentiable due to the jagged nature of random movements. Each time step increment $W(t) - W(s)$ is independent and has a normal probability distribution with a mean of 0 and a variance of $t - s$ for all $0 \le s \le t < \infty$. Therefore, $W(t)$ is a normal random variable with mean 0 and variance t that satisfies

$$
dW(t) = W(t + dt) - W(t).
\tag{3.3}
$$

We can now define the noise term $N(t) \cdot dt = dW(t)$. This notation is equivalent to $N(t) = \frac{dW(t)}{dt}$, or the derivative of the Wiener process. According to Professor Logan from University of Nebraska [12], while the Wiener process is not differentiable and therefore does not have a classical derivative, the Wiener process does have a generalized derivative called **white noise**. Replacing this noise term into the exponential differential equation with additive noise (3.1), we get

$$
dX(t) = rX(t)dt + \sigma dW(t),
\tag{3.4}
$$

where σ indicates the intensity of the noise term that is being added. This equation is the classic example of a stochastic differential equation (SDE). There are two main versions of stochastic differential equations: Itô SDE and Stratonovich SDE [2]. They can be converted into each other; however, to remain consistent and use only one type of numerical approximator in this project, the Itô SDE will be used.

3.2   Itô Stochastic Process

An SDE is said to be an Itô SDE if for all $t > 0$:

$$
\begin{aligned}
dX(t) &= a\big(X(t), t\big)dt + b\big(X(t), t\big)dW(t) \\
X(0) &= X_0 \text{ (an initial condition)},
\end{aligned}
\tag{3.5}
$$

where a and b are given functions of $X(t)$ and t. For example, Equation 3.4 satisfies an Itô SDE, where $a = rX(t)$ and $b = \sigma$, which is a constant.

Many Itô SDEs can be solved for by hand using Itô's Lemma (see Chapter 8 of Allen, 2001 [2] and Chapter 7 of Logan, 2009 [12] for more information on the properties and solutions of Itô SDES). However, for complicated SDEs like the models we have been using, solving for the solution by hand would be next to impossible. A numerical procedure called the **Euler–Maruyama method** approximates an Itô SDE by a discrete process. First, a partition of N subintervals is chosen so that for each of the $n = 0, 1, 2, \ldots, N$ subintervals, the partition size is equal to Δt and $t_n = n\Delta t$.

The Euler–Maruyama discretization of the general Itô equation (see Equation 3.5) is then

$$
X_{n+1} = X_n + a(X_n, t_n)\Delta t + b(X_n, t_n)(W_{n+1} - W_n).
\tag{3.6}
$$

where $n = 0, 1, 2, \ldots, N-1$. The Euler–Maruyama discretization of the exponential SDE (see Equation 3.4) is

$$
X_{n+1} - X_n = rX_n\Delta t + \sigma(W_{n+1} - W_n).
\tag{3.7}
$$

where $n = 0, 1, 2, \ldots, N - 1$ [12].

Since $W_{n+1} - W_n \approx dW(t)$, and we know from the properties of the Wiener process (see Subsection 3.1) that $W(t)$ is a normal random variable with mean 0 and variance t, then we can say that

$$
W_{n+1} - W_n = \sqrt{\Delta t} \cdot Z_n, \text{ where } Z_n \sim N(0, 1).
\tag{3.8}
$$

Therefore, the noise term $W(t)$ can be discretized as a random standard normal with a standard deviation of $\sqrt{\Delta t}$.

We now have enough information to code discretized versions of SDEs on MATLAB and solve them. One way to add stochasticity is to directly add a Wiener process to the differential equations representing phytoplankton and zooplankton. The MATLAB code `PZ_matlab_EM.m` [1] uses the Euler–Maruyama method to numerically approximate these stochastic differential equations us-
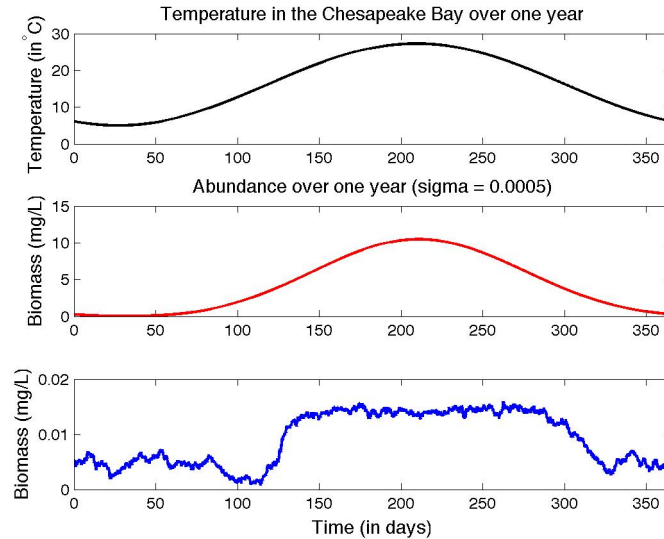
ing $\sigma = 0.0005$ (see Figure 3.1).

Figure 3.1: *Plot of the P-Z model (2.3) over the course of one year with initial conditions $[P, Z] = [0.25, 0.005]$ mg/L, $\sigma = 0.0005$, and $N = 100,000$. Same rates and constants as Figures 2.2 (see Appendix A.3).*

Because the zooplankton are approximately three orders of magnitude less abundant than the phytoplankton, the zooplankton are more affected by the stochasticity in this model. The σ value indicating the noise term is the same when applied to both the phytoplankton and zooplankton equations. A more mechanistic way of adding in stochasticity would be to create a third differential equation representing temperature and adding in the stochasticity to that equation using an Ornstein–Uhlenbeck Process.

3.3 Ornstein–Uhlenbeck Process

The Wiener process is a random walk in continuous time. The Ornstein-Uhlenbeck process, on the other hand, is a stochastic process that is a modified version of the Wiener process. The Ornstein-Uhlenbeck process describes the random velocity of a Brownian particle, but under "friction." Under this process the random Brownian particle will not stray too far from its general trend or average. Because we are modifying temperature, we are not interested in a random walk. We do not want the temperature to sometimes randomly move extremely far away from its general cosine trend. The following Figure 3.2 is a graph of the temperature function under the standard Wiener process. As can be seen in the figure, the stochastic

temperature curve can sometimes vastly overestimate or underestimate the actual temperatures due to the random-walk nature of the Wiener process, sometimes exceeding 40 °C when the surface water temperature should not exceed about 28 °C in the Chesapeake Bay [7].
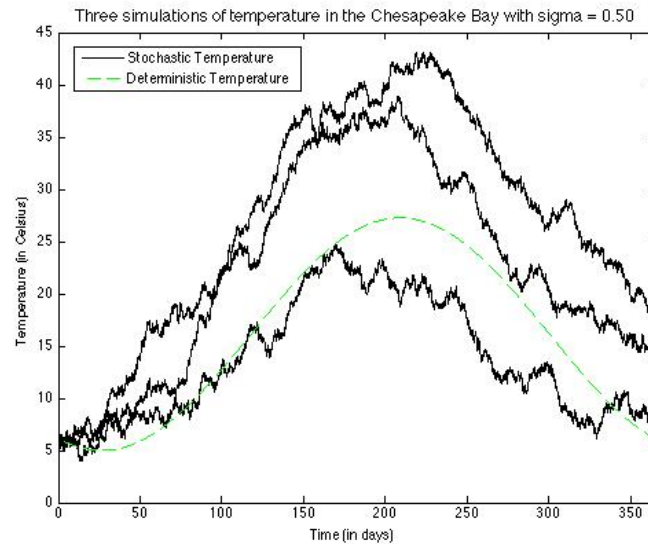

Figure 3.2: *Plot of the deterministic water temperature in the Chesapeake Bay using temperature function (2.2) and three simulations of stochastic water temperature under the Wiener process with $\sigma = 0.5$.*

A stochastic differential equation with the Wiener process does not work for adding noise to temperature. We need a stochastic process with a *mean-reverting* property in order for the temperature, while fluctuating randomly, to still follow its general cosine trend of being higher in the summer than it is in the winter on average. The Ornstein-Uhlenbeck process is the simplest stochastic process with this mean-reverting property. It is the only stochastic process that is stationary, Gaussian, and Markovian [5] [18].

The first property, **stationary**, indicates that the joint probability distribution does not change over time or over space. Therefore, the mean and variance of the noise terms remain the same over time. While the mean and variance of stochastic changes in temperature may actually change over time in the real world, the stationary property is a strong and simplifying assumption we must take. The second property, **Gaussian**, signifies that the random variations follow a normal distribution. It is reasonable for the random fluctuations to follow a normal distribution, as we would expect small variations in temperature to be much more common than large variations. The third property, **Markovian**, is a mathematical property that indicates that the stochastic process is "memoryless." This memoryless property

argues that one can make predictions on the future based on the present state just as well as one could if they had the entire history of previous states. For example, if I know the temperature on August 1st I could make an equally valid prediction for the temperature on September 1st as I could if I knew the temperature of every single day leading up to August 1st [5, 6, 18].

The general form of the Ornstein–Uhlenbeck process is

$$dX(t) = \theta(\mu - X(t))dt + \sigma dW(t), \tag{3.9}$$

where $X(t)$ is the state variable that is being modified with stochasticity. The parameters θ and σ must be greater than 0, and μ is the average of the state variable. The parameter θ indicates the intensity of the pull towards the average, or the strength of the mean reversion. The larger the θ, the stronger the mean reversion becomes. The constant σ indicates the magnitude of the noise being added. Finally, $dW(t)$ is the standard Wiener process (3.3).

The Euler–Maruyama approximation of the Ornstein-Uhlenbeck process is

$$X_{n+1} = X_n + \theta(\mu_n - X_n)\Delta t + \sigma(W_{n+1} - W_n), \tag{3.10}$$

where $X_n = X(n\Delta t)$, $\mu_n = \mu(n\Delta t)$, and $W_n = W(n\Delta t)$. By (3.8), we know that $W_{n+1} - W_n = \sqrt{\Delta t} \cdot Z_n$ where $Z_n \sim N(0, 1)$.

In order to apply the Ornstein–Uhlenbeck process to our P-Z model (2.3), set the variable $X(t)$ to be the state variable representing temperature. Set $\mu \equiv \mu(t)$ as the deterministic temperature function (2.2), or the "average" trend that the stochastic differential equation should be reverting to. Set Δt as small as possible while still having a reasonable run-time in MATLAB. And finally, vary the parameters θ and σ to see the effect of stochasticity on temperature.

3.4 Modified Ornstein–Uhlenbeck Process

The Ornstein–Uhlenbeck process mentioned in the previous section (see Section 3.3) functions in MATLAB as intended. The temperature fluctuates around the given deterministic temperature function $\mu(t)$, with larger fluctuations if the parameter σ becomes larger. However, the literature suggests a slight modification is needed in order for the Ornstein–Uhlenbeck process to properly work when modeling temperature. The main mathematical issue is that the Ornstein-Uhlenbeck process's mean-reverting property is meant to revert to a constant rather than a changing mean. Since the temperature function has a changing mean throughout the course of a year, there will be some bias when using this process.

Dornier and Querel [6] proved that the only way for the bias to be 0 is if the

mean is constant. They also proved that adding a simple term to the Ornstein–Uhlenbeck process would eliminate this bias. The term added in is the derivative of the mean, since the mean is what is changing over time. Therefore, the general form of the modified Ornstein–Uhlenbeck process is

$$dX(t) = d\mu(t) + \theta(\mu(t) - X(t))dt + \sigma dW(t). \tag{3.11}$$

The Euler–Maruyama approximation for the modified Ornstein-Uhlenbeck process is

$$X_{n+1} = X_n + \Delta\mu_n + \theta(\mu_n - X_n)\Delta t + \sigma\sqrt{\Delta t} \cdot Z_n, \tag{3.12}$$

where $\Delta\mu_n = \mu_{n+1} - \mu_n$ and $Z_n \sim N(0,1)$.

3.5 Stochastic Simulations

Using the numerical approximation of the modified Ornstein–Uhlenbeck process in MATLAB, we can simulate the temperature in the Chesapeake Bay with added in random variation. Using the stochastic temperature function, we can also see what happens to the phytoplankton and zooplankton over time. With added stochasticity, is there a chance that either species could go extinct?

3.5.1 Stochastic P-Z Model Runs

The P-Z model with cannibalism (2.3) was run with a stochastic temperature function using the Euler–Maruyama approximation for the modified Ornstein–Uhlenbeck process (see Equation 3.12). The code for these simulations can be found at `PZT_matlab_EM_par.m` [1]. The following figures (3.3) show one run of the model over the course of a year with varying values set for σ, which indicates the magnitude of stochasticity in the temperature.

Figure 3.3: *Plots of the P-Z model with $\sigma = 0, 0.5, 1, \ldots, 6$. The top subplot displays the deterministic and stochastic water temperature, the middle subplot displays the deterministic and stochastic phytoplankton biomass, and the bottom subplot displays the deterministic and stochastic zooplankton biomass in the Chesapeake Bay.*
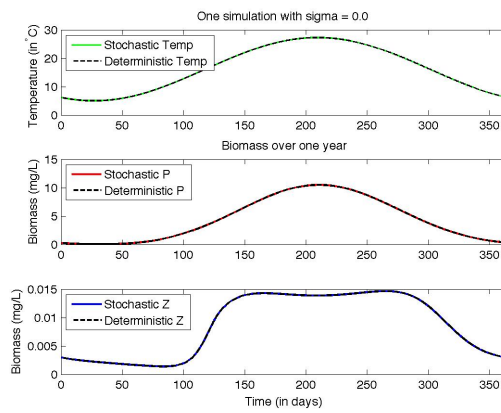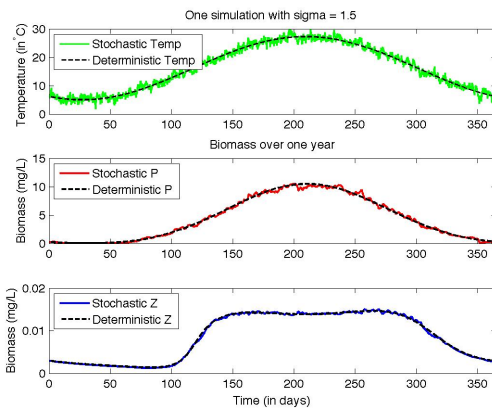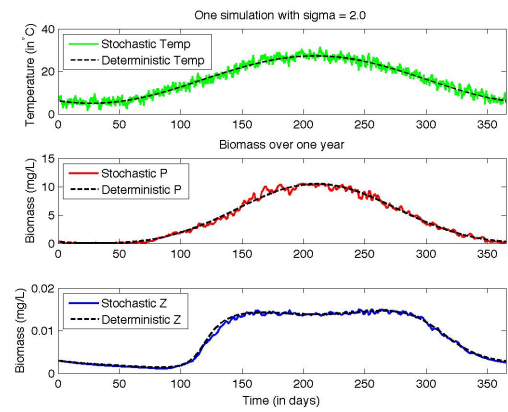

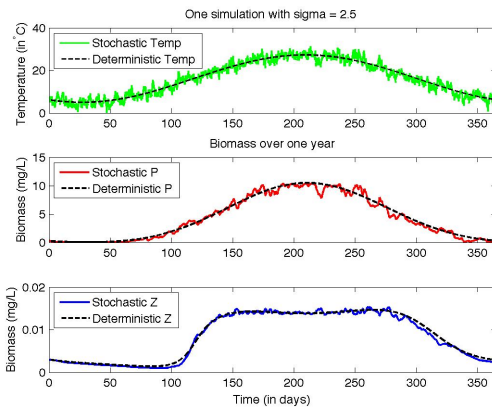(a) Plot with $\sigma = 0.0$.
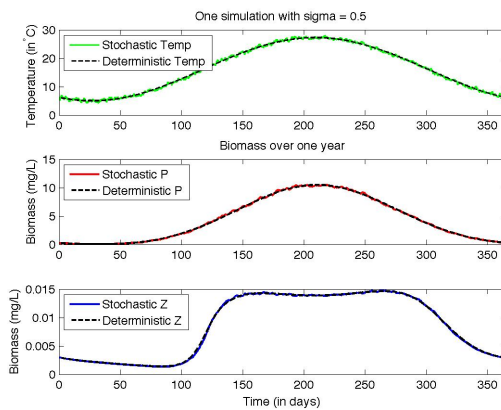
(b) Plot with $\sigma = 0.5$.
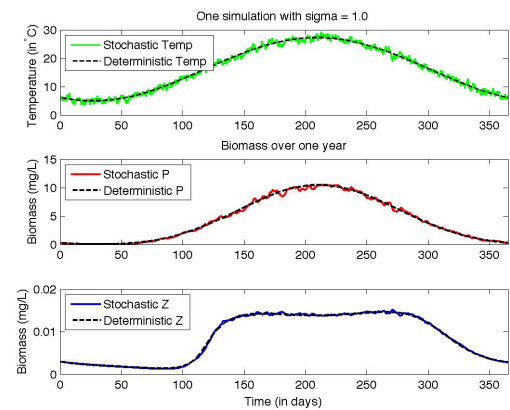
(c) Plot with $\sigma = 1.0$.
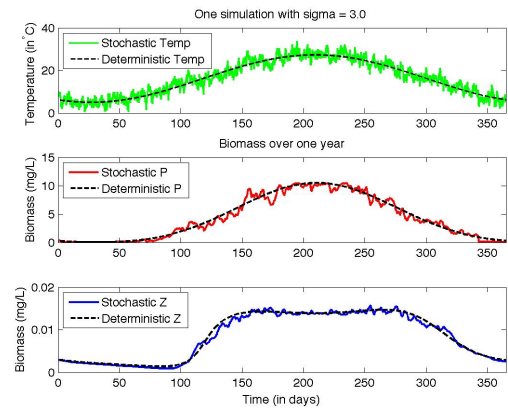
(d) Plot with $\sigma = 1.5$.

(e) Plot with $\sigma = 2.0$.
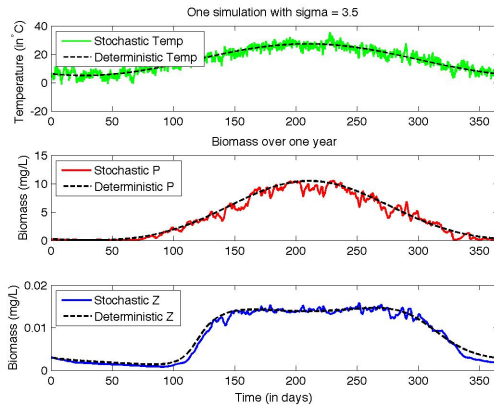
(f) Plot with $\sigma = 2.5$.
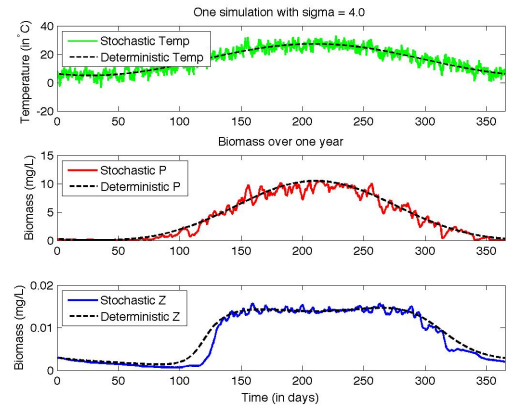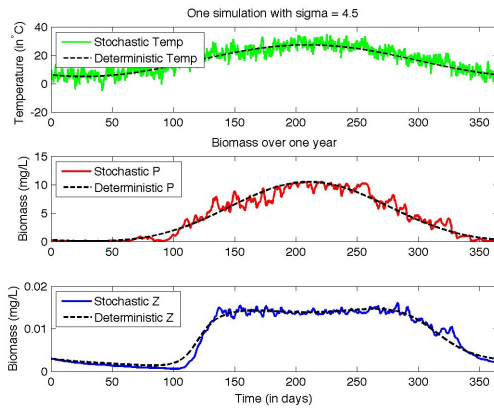
(g) Plot with $\sigma = 3.0$.

(h) Plot with $\sigma = 3.5$.

(i) Plot with $\sigma = 4.0$.

(j) Plot with $\sigma = 4.5$.
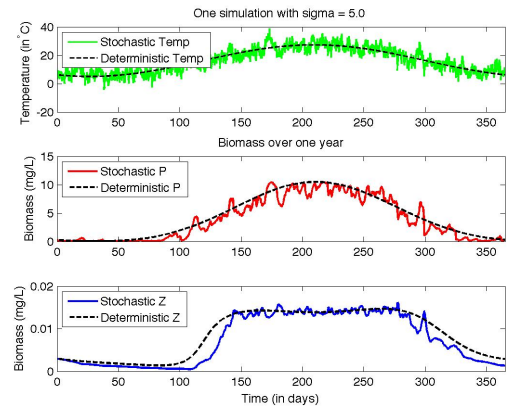
(k) Plot with $\sigma = 5.0$.
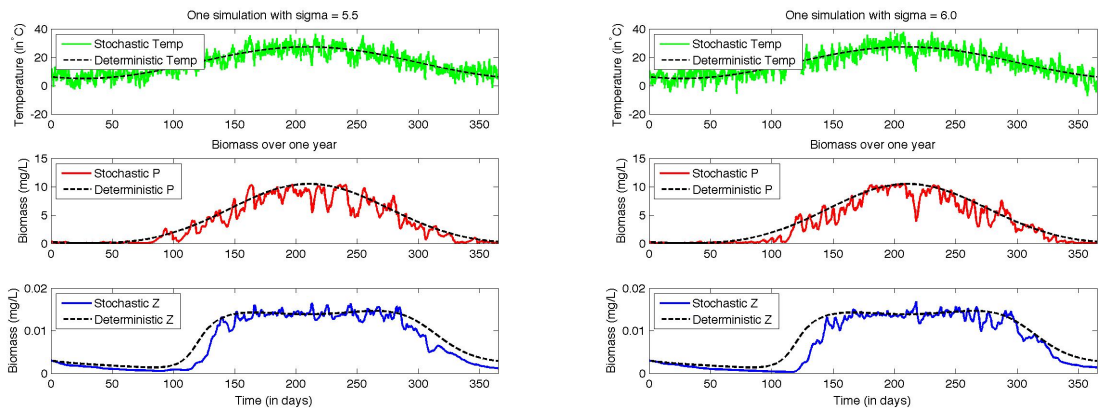
(l) Plot with $\sigma = 5.5$.   (m) Plot with $\sigma = 6.0$.

3.5.2   Stochastic Time-T Maps

The graphs in Figure 3.4 are time-t maps in which nine initial conditions are tested. One of the initial conditions tested is the fixed point $(0.2844, 0.0029)$ mg/L (as determined by the deterministic system, code found at `PZ_matlab_par.m` [1]). The other eight points tested form a box around the fixed point $[0.0345 - 0.5345, 0.0004 - 0.0054]$, a plus and minus distance of 0.25 and 0.0025 for the phytoplankton and zooplankton respectively. The horizontal axis represents the phytoplankton biomass while the vertical axis represents the zooplankton biomass. The percents next to each of the nine initial conditions indicate the percent of the 1000 stochastic simulations done at that initial point that go extinct. The figures also display what percent of total simulations end up inside the box of initial conditions and what percent end up outside the box of initial conditions. Finally in the legend, the % OOB indicates the percent of simulations whose final coordinates are out of the bounds of the graph. The code for these simulations can be found at `PZT_Simulations_par.m` [1].

As can be seen in the plots in Figure 3.4, the extinction rate is virtually 0 until σ reaches 6. When analyzing Elliott and Tang Chesapeake Bay temperature data [7] and the EPA Chesapeake Bay monitoring program data [3], the most realistic value for this parameter is $\sigma = 1.5$. Therefore, even under realistic stochasticity, the system is still strongly contracting.

Figure 3.4: *Time-t maps of the stochastic P-Z model with $\sigma = 0, 0.5, 1, \ldots, 6$. Nine initial conditions are simulated 1000 times each and mapped to their final coordinates after one year. The red point is the deterministic fixed point and the eight black points are the other initial conditions. The percents next to each of the initial points indicate the percent of simulations starting from that point that go extinct. The percent inside the box indicates the percent of simulations that remain within the box of initial conditions.*
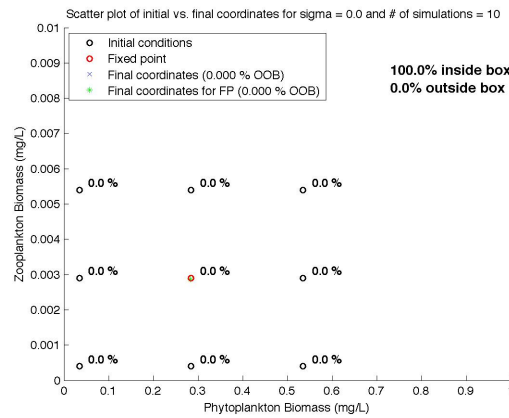
(a) Time-t map of the model with $\sigma = 0.0$.
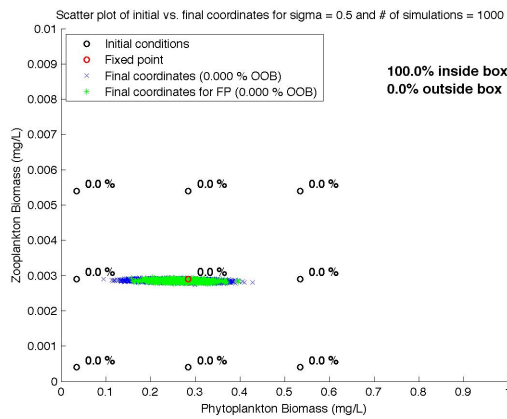
(b) Time-t map of the model with $\sigma = 0.5$.
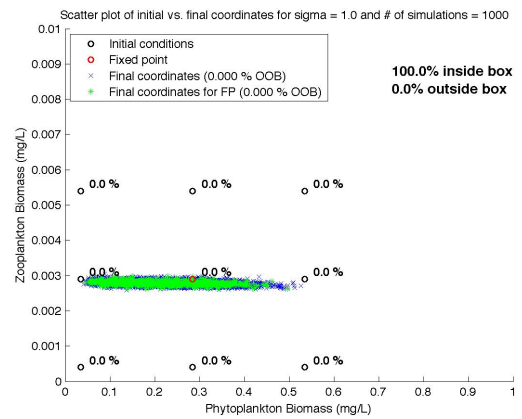
(c) Time-t map of the model with $\sigma = 1.0$.
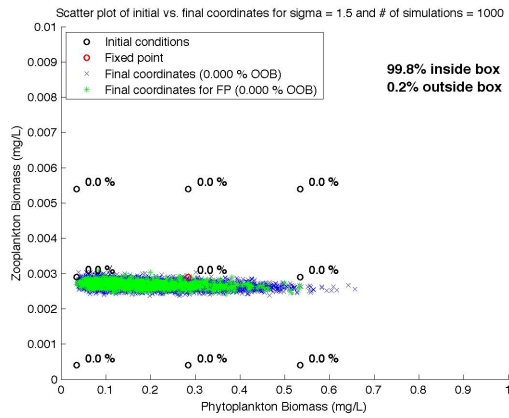
(d) Time-t map of the model with $\sigma = 1.5$.
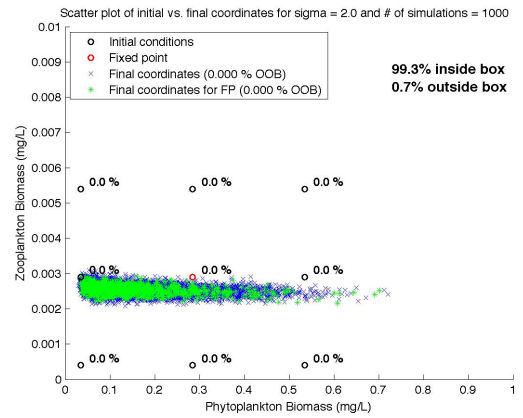
(e) Time-t map of the model with $\sigma = 2.0$.
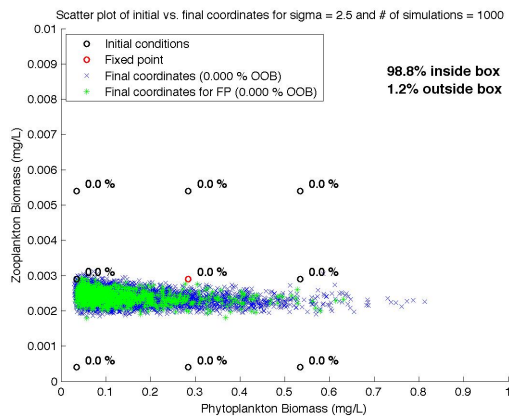
(f) Time-t map of the model with $\sigma = 2.5$.
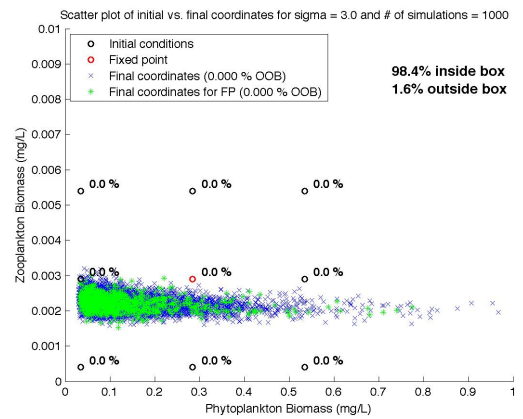
(g) Time-t map of the model with $\sigma = 3.0$.
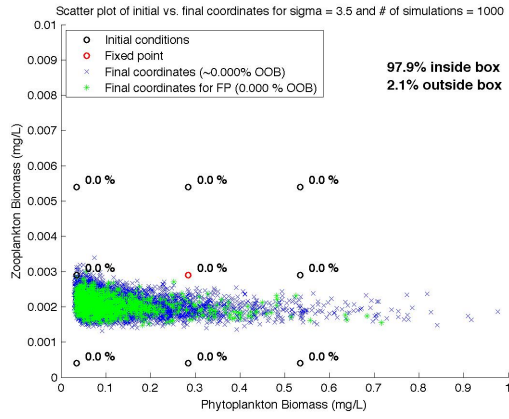
(h) Time-t map of the model with $\sigma = 3.5$.
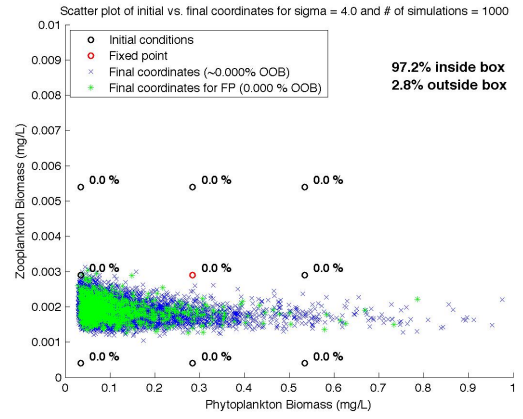
(i) Time-t map of the model with $\sigma = 4.0$.
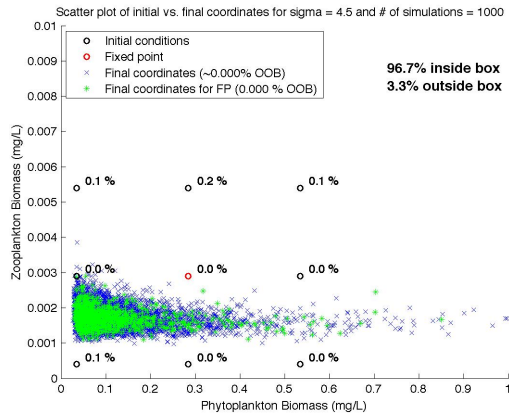
(j) Time-t map of the model with $\sigma = 4.5$.
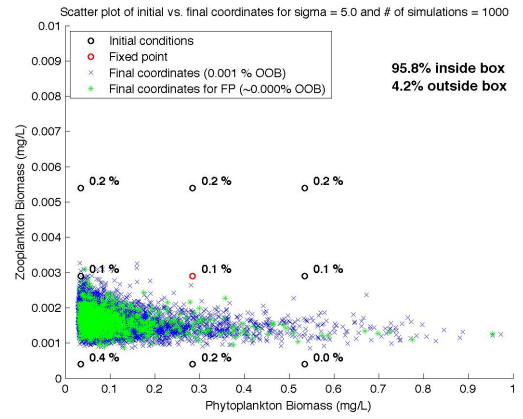
(k) Time-t map of the model with $\sigma = 5.0$.
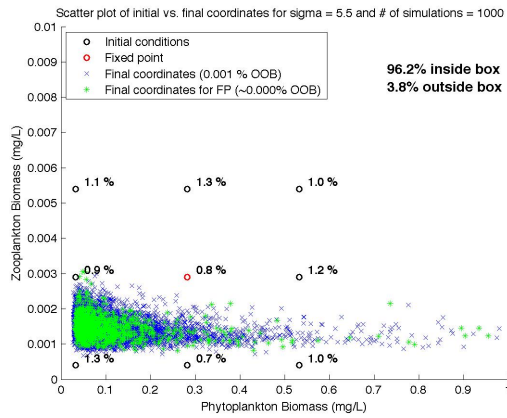
(l) Time-t map of the model with $\sigma = 5.5$.   (m) Time-t map of the model with $\sigma = 6.0$.
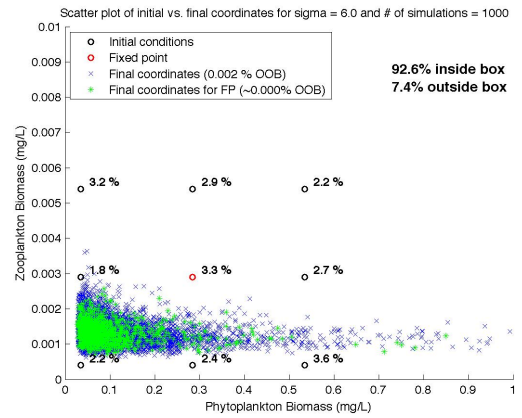
At each value of σ, the extinction rate was calculated at each of the initial conditions. More simulations were run with σ set to more unrealistic values of 7, 8, 9, and 10. Figure 3.5 shows the percent of overall simulations that go extinct for σ ranging from 0 to 10. For each value of σ, 9000 simulations were run (1000 for each of the nine initial conditions).
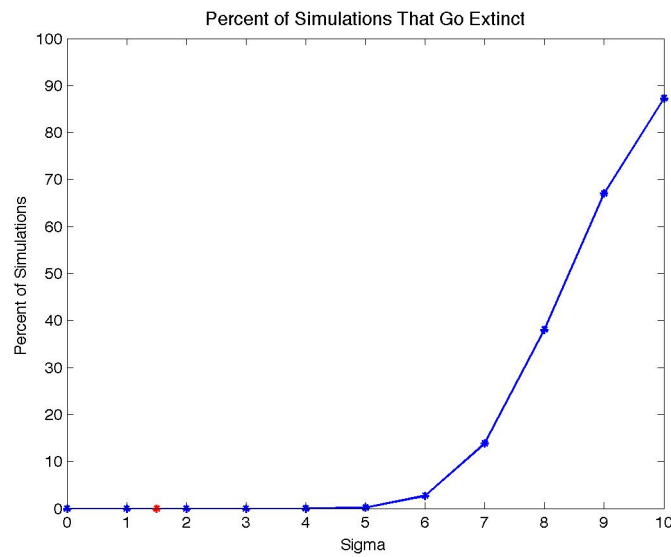
Figure 3.5: *Percent of simulations that go extinct for $\sigma = 0, 1, 2, \ldots, 10$. The red point indicates the most biologically realistic value for σ according to [3].*

Chapter 4

Conclusion

4.1 Summary

Zooplankton play a crucial role in aquatic ecosystems, and their mortality terms have not been well-studied [7]. In order to better understand the effects of different types of mortality, we built a nonlinear differential equation model that incorporated non-predatory mortality, predatory mortality, and cannibalism. Our P-Z model (2.3) predicted the correct order of magnitude for both the phytoplankton and the zooplankton in the Chesapeake Bay (see Figure 2.2). Additionally, the model predicted peaks in both species during the annual cycle roughly the same time that they peak in nature. The model suggests two weak peaks for the zooplankton, one in the late spring and one in late summer, and this result is in line with previous studies [16]. Because this model incorporates the three main causes of mortality, it may serve as a base for further hypothesis testing and accurate zooplankton model construction.

As can be seen in simulations of the time-t maps (see Figure 3.4), this system appears to be relatively stable. Close to 100% of the simulations remain centered around the fixed point for the deterministic system, indicating general contraction in this neighborhood. The extinction rate is virtually 0 until σ, the magnitude of the stochasticity, reaches about 6. When analyzing the EPA Chesapeake Bay temperature data from 1989–2009, a feasible value for this parameter is $\sigma = 1.5$ [3]. When $\sigma = 1.5$, there is virtually a 0% extinction rate, and approximately 99.8% of the simulations remain within the box of initial conditions.

Therefore, even under a realistic amount of stochasticity, the system still appears to be strongly contracting, though the iterations appear to be moving towards $(P, Z) = (0, 0)$ the higher the stochasticity. This result is a good sign for the phytoplankton and zooplankton communities in the Chesapeake Bay area, and for the populations that depend on zooplankton as a food source. Unless

the surface water temperature changes drastically, model simulations suggest only a small risk of this system collapsing. Because this project addressed only one environmental condition (temperature), results could change with multiple conditions changing.

4.2   Future Work

There are a few future directions for this phytoplankton-zooplankton dynamics research. First, we are interested in analyzing the contraction rates on the time-t maps. When mapping initial conditions from the fixed point, we end up with a distribution of images of the fixed point. In the deterministic system, the images are always mapped to the fixed point, but when stochasticity is added the average value of the mapping of the images shifts towards the origin as stochasticity is increased. Is the deterministic fixed point still attracting in the stochastic system? At what rate are the final coordinates approaching the origin under stochasticity?

We are also interested in further analyzing the stage structure in the phytoplankton-zooplankton model because zooplankton cannibalize only on zooplankton that are smaller and younger than them. We created a two-stage zooplankton model (2.8), but only studied stochastic time-t maps for the P-Z model (2.3). Would adding in stage structure change the dynamics of the model? Does the increase in accuracy offset the decrease in the mathematical tractability of the model?

Another interesting direction for this research would be to improve the accuracy of the parameters in the model. Many of the rates were derived from studies that considered zooplankton species other than *Acartia tonsa* zooplankton, which is the dominant species in the Chesapeake Bay. Experiments on *Acartia tonsa* could be run to more accurately measure their mortality and cannibalism rates. But how precise must the parameters be while still being able to say something about the model and the predictions it makes? Another way to look at the accuracy of the parameters would be to quantify the uncertainty. Performing uncertainty quantification would allow us to study the robustness of the results with respect to perturbations of the parameters. This type of analysis could give meaningful results, indicating that the phytoplankton and zooplankton populations would be within a certain range of values after a year even if the estimated parameters were off by a specified, fixed amount.

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Appendix A

Rates, Constants, and Data

A.1   Phytoplankton Data

Table A.1 shows the average phytoplankton biomass in mg/L over the course of the year 2000:

Table A.1: Phytoplankton biomass data

Day	Biomass (mg/L)	Day	Biomass (mg/L)
12	0.397743313	172	1.348665771
19	0.8600254682	187	1.887869968
32	0.5111397695	196	0.7403359089
39	0.6553646326	200	6.171838117
47	0.7447532962	220	0.3098471799
53	0.3277020758	221	1.155309049
54	0.3594423693	235	11.52763205
67	3.648309749	237	0.2035418994
76	0.2165858805	258	0.9113419987
89	0.4719253896	269	0.9341463973
104	0.783696934	273	1.258085071
115	1.647043722	284	0.2243664086
117	0.6233190573	298	3.465217802
130	1.47688918	312	0.2782209264
132	0.4535744615	321	0.1371734286
144	0.5629005326	333	2.666820833
147	0.1987690721	341	0.3022513362
158	1.3916321	348	2.065213408
164	0.3745450645	349	0.1379906322

The data used to estimate the phytoplankton growth rate and carrying capacity were taken from the Chesapeake Bay Program (`http://chesapeakebay.net/data`). The data were collected from January 2000 to October 2002 in the York and James Rivers and consist of the abundance per liter for many species of phytoplankton. Kate Shipman, the biology undergraduate on this project, converted the abundance data to biomass data in units of mg/L using the conversion factor $3.864 \cdot 10^{-5}$. The data in the above table are from the year 2000 only and were plotted in order to estimate the carrying capacity of phytoplankton.

A.2 Zooplankton Data

Table A.2 shows the average monthly zooplankton biomass in mg/L over the years 2000-2002:

Table A.2: Zooplankton biomass data

Day (monthly average)	Biomass (mg/L)
15	0.0035062
45	0.0032194
75	0.0027213
105	0.0128653
135	0.0027189
165	0.0016145
195	0.0109381
225	0.0051234
255	0.0181035
285	0.0170578
315	0.0130936
345	0.0027154

The data were taken from the Chesapeake Bay Program (`http://chesapeakebay.net/data`). The zooplankton data measure the abundance of the copepods and adults in the water column. The abundance data from the program were converted to biomass data in units of mg/L using conversion factors taken from [8].

A.3 P-Z Model Rates and Constants

The MATLAB code used to plot the figures in this paper used the model from Equation 2.3 and the following rates and constants, which were derived from the literature or from the publicly available zooplankton and phytoplankton abundance data from the Chesapeake Bay Program (CBP). The data can be found at `http://www.chesapeakebay.net/data`.

	Units	Value	Source
Day in model (t)	days	1 to 365	
Temperature (T)	° C	$16.133 - 11.132 \cdot \cos[2\pi(t + 28.076)/365]$	[7]
$r(T)$	day^{-1}	$[0.25 - 0.75]$ (linear function of T)	[16]
r_{avg}	day^{-1}	0.5 (average of $r(T)$)	[16]
$K(T)$	mg L^{-1}	$[0.05 - 7]$ (linear function of T)	[16] & CBP
g	day^{-1}	1.359	Fit to [11]
μ	mg L^{-1}	0.5381	Fit to [11]
b		0.6	[16]
m	day^{-1}	$0.00585 \cdot T - .04172$	[7] [8]
γ	day^{-1}	$[1 - 10]$ (linear function of T)	Fit to [11]
k	mg L^{-1}	0.5	[16]
c_z		0.9876	Fit to [11]
c_p		0.0124	Fit to [11]

Shipman worked on finding realistic parameters for this P-Z model. She looked through the literature and used data from published papers to come up with rates and constants for this model. She also directly considered the phytoplankton and zooplankton data collected in the Chesapeake Bay to better estimate phytoplankton carrying capacity and growth rates. The following is a list of estimated biologically realistic rates that we use in our P-Z model with cannibalism:

- *Carrying capacity of the phytoplankton, $K = 0.05 - 7 \, mg/L$* is a linear function of temperature. In Scheffer's paper [16] he estimated the carrying capacity to have a maximum of 10 mg/L, but analyzing the phytoplankton data in the Chesapeake Bay, a lower carrying capacity appears more likely (Appendix A.1).

- *Growth rate of the phytoplankton, $r = 0.25 - 0.75$ day^{-1}* is a linear function of temperature and $r_{avg} = 0.5$. In Scheffer's paper [16] he estimated r_{avg} to be 0.5. With little information on phytoplankton growth rate, this range was

estimated and r_{avg} is kept the same as in Scheffer's paper [16].

- *Non-predatory zooplankton mortality, $m = 0.00585 \cdot T - 0.04172$.* This equation is taken from Elliott and Tang's [7] non-predatory mortality rate where T stands for the temperature in the Chesapeake Bay. This equation is the weighted average of the nauplii mortality equation and the copepods/adults mortality equation then scaled by the average biomass of nauplii and copepods/adults [8].

- *Percentage of grazing that goes to growth, $b = 0.6$.* We kept this value the same as in Scheffer's paper [16].

- *Half-maximum constant for higher trophic grazing, $k = 0.5$.* We kept this value the same as in Scheffer's paper [16].

For the constants c_p, c_z, g, and μ, Shipman used data from [11] and ran two different fits, one for the prey choice parameters (c_p and c_z) remaining constant and another fit in which the prey choices depend on the ratio of P and Z in the water column (see Section 2.2 for more information on the two different hypotheses). The R^2 for the first fit was 0.4597 and for the second fit was 0.4205. The constants Shipman found through these fits were

- *Maximal zooplankton grazing rate, $g = 1.359$ day^{-1} for the constant hypothesis and $g = 1.217$ day^{-1} for the ratio-dependent hypothesis.*

- *Half-maximum constant for predation on zooplankton and phytoplankton, $\mu = 0.538$ mgL^{-1} for the constant hypothesis and $\mu = 0.5476$ mgL^{-1} for the ratio-dependent hypothesis.*

- *Relative preference zooplankton have for eating other zooplankton, $c_z = 0.9876$ in the constant hypothesis.*

- *Ratio-dependent prey choice, $a = 0.002701$, for the ratio-dependent hypothesis.*

- *The higher trophic grazing rate $\gamma = 1 - 10$ mg day^{-1} for the constant prey choice hypothesis and $\gamma = 5 - 15$ mg day^{-1} for the ratio-dependent prey choice (2.5).* There was no literature on this parameter, so we estimate it to fit the phytoplankton and zooplankton data.

Neither fit has a particularly high R^2 value, and the ratio-dependent prey choice has parameter a as very low indicating that the ratio between P and Z matters little in the prey choice functions. However, finding that $c_z = 0.9876$ in the constant prey choice hypothesis is surprising. This constant indicates that when given

the choice almost 99% of the time, zooplankton prefer to eat other zooplankton. This prey choice constant does not mean that they eat other zooplankton 99% of the time, just that they prefer them. It is possible that they do prefer eating other zooplankton, since zooplankton have a higher mass and perhaps more nutrition. They will not be able to eat zooplankton even close to 99% of the time, as phytoplankton biomass is about three orders of magnitude more prevalent in the water column (Appendix A.1 and A.2). Finally, if and when we get information on higher trophic grazing either through the literature or through experiments Shipman is planning to run, we may be able to determine which prey choice parameter hypothesis is more accurate. At this time, the constant and the non-constant prey choice hypotheses seem equally valid when plotted against data. Therefore, the constant prey choice hypothesis was chosen as it has one fewer parameter than the non-constant prey choice hypothesis.

A.4   P-Z-Z Model Rates and Constants

The MATLAB code used to plot the figures in this paper used the model from Equation 2.8 and the following parameters, which were derived from the literature or from the publicly available zooplankton and phytoplankton abundance data from the Chesapeake Bay Program (CBP).

	Units	Value	Source
Day in model (t)	days	1 to 365	
Temperature (T)	° C	$16.133 - 11.132 \cdot \cos[2\pi(t + 28.076)/365]$	[7]
$r(T)$	day^{-1}	$[0.25 - 0.75]$ (linear function of T)	[16]
r_{avg}	day^{-1}	0.5 (average of r(T))	[16]
$K(T)$	mg L^{-1}	$[0.05 - 7]$ (linear function of T)	[16] & CBP
g	day^{-1}	1.359	Fit to [11]
μ	mg L^{-1}	0.5381	Fit to [11]
d	day^{-1}	$(3 \cdot 1.05 + 3 \cdot 0.81) \cdot (5491.85/11)) \cdot (T + 0.96)^{(-2.05)}$	Modified from [7]
b		0.6	[16]
m_0	day^{-1}	$(1.707 \cdot 10^{-4}) \cdot T + (2.275 \cdot 10^{-4})$	[7] [8]
m_1	day^{-1}	$0.011459 \cdot T - .083669$	[7] [8]
γ	day^{-1}	$[1 - 10]$ (linear function of T)	Fit to [11]
k	mg L^{-1}	0.5	[16]
c_z		0.9876	Fit to [11]
c_p		0.0124	Fit to [11]

Most of the rates and constants in the P-Z-Z model are the same as those in the P-Z model (Appendix A.3). The main changes include having two different non-predatory mortality rates, m_0 for the immature zooplankton class and m_1 for the zooplankton class, and a development rate d between those two zooplankton classes:

- *Non-predatory immature zooplankton mortality*, $m_0 = 1.707 \cdot 10^{-4} \cdot T + 2.275 \cdot 10^{-4}$. This equation is taken from Elliott and Tang's [7] naupliar non-predatory mortality rate where T stands for the water temperature in the Chesapeake Bay. This naupliar non-predatory mortality equation is scaled by the average biomass of nauplii [8].

- *Non-predatory mature zooplankton mortality*, $m_1 = 0.0115 \cdot T - 0.0837$. This equation is taken from Elliott and Tang's [7] copepodite and adult non-predatory mortality rate where T stands for the water temperature in the Chesapeake Bay. This mature non-predatory mortality rate equation is scaled by the average biomass of the copepods and adults [8].

- *Development rate from nauplii to copepod/adult*:

$$d = 1/((3 \cdot 1.05 + 3 \cdot 0.81)(5491.85/11)(T + 0.96)^{-2.05}).$$

This equation is taken from Elliott and Tang's [7] development rates. The 1.05 refers to the stage duration of nauplii I classes and is multiplied by 3 since Elliott and Tang's model had 3 nauplii I classes. The 0.81 refers to the stage duration of the nauplii II classes and is also multiplied by 3.

Appendix B

Nondimensionalization of P-Z Models

B.1 P-Z Model

To nondimensionalize the P-Z model with cannibalism (Equation 2.3), let $P = \alpha \tilde{P}$, $Z = \beta \tilde{Z}$, and $t = \tau \tilde{t}$. Then $d\tilde{P} = \frac{1}{\alpha} dP$, $d\tilde{Z} = \frac{1}{\beta} dZ$, and $d\tilde{t} = \frac{1}{\tau} dt$. It is important to note the units of the original rates and constants in order to verify that the nondimensionalized rates and constants are truly unitless. Rates, constants, and variables K, k, μ, P, and Z are in units of abundance. Rates g, r, m are in units of $\frac{1}{time}$. Rate γ is in units of $\frac{abundance}{time}$. Constants b, c_p, and c_z are already unitless. First, nondimensionalize the first differential equation:

$$
\begin{aligned}
\frac{d\tilde{P}}{d\tilde{t}} &= \frac{\tau}{\alpha} \frac{dP}{dt} = \frac{\tau}{\alpha} \left[r\alpha \tilde{P}\left(1 - \frac{\alpha \tilde{P}}{K}\right) - g\left(\frac{c_p \alpha^2 \tilde{P}^2}{\mu^2 + c_p \alpha^2 \tilde{P}^2 + c_z \beta^2 \tilde{Z}^2} \beta \tilde{Z}\right) \right] \\
&= \tau r \tilde{P}\left(1 - \frac{\alpha \tilde{P}}{K}\right) - \frac{g\tau c_p \alpha \tilde{P}^2 \beta \tilde{Z}}{\mu^2 + c_p \alpha^2 \tilde{P}^2 + c_z \beta^2 \tilde{Z}^2}.
\end{aligned}
$$

Let $\tau = \frac{1}{r}$, $\alpha = K$, and $\beta = K$, and take out an $\frac{\alpha \beta}{\alpha \beta}$ from the last term to get

$$
\frac{d\tilde{P}}{d\tilde{t}} = \tilde{P}(1 - \tilde{P}) - \frac{gc_p}{r}\left(\frac{\tilde{P}^2 \tilde{Z}}{\frac{\mu^2}{K^2} + c_p \tilde{P}^2 + c_z \tilde{Z}^2}\right).
$$

Choose nondimensionalized functions of temperature $f = \frac{g}{r}$ and $h^2 = \frac{\mu^2}{K^2}$. When the original units of the rates g, r, μ, and K are used as arguments in f and h^2, we can see that f and h^2 are unitless. Therefore, the final nondimensionalized

version of the differential equation for phytoplankton is

$$\frac{d\tilde{P}}{d\tilde{t}} = \tilde{P}(1 - \tilde{P}) - c_p f \frac{\tilde{P}^2 \tilde{Z}}{h + c_p \tilde{P}^2 + c_z \tilde{Z}^2}. \tag{B.1}$$

Using the same values for $\tilde{P}$, $\tilde{Z}$, and $\tilde{t}$, and letting $\tau = \frac{1}{r}$ and $\alpha = \beta = K$ as used in the previous equation, we can also nondimensionalize the zooplankton differential equation:

$$
\begin{aligned}
\frac{d\tilde{Z}}{d\tilde{t}} &= \frac{\tau}{\beta}\left[bg \frac{c_p \alpha^2 \tilde{P}^2 + c_z \beta^2 \tilde{Z}^2}{\mu^2 + c_p \alpha^2 \tilde{P}^2 + c_z \beta^2 \tilde{Z}^2} \beta \tilde{Z} - g \frac{c_z \beta^2 \tilde{Z}^2}{\mu^2 + c_p \alpha^2 \tilde{P}^2 + c_z \beta^2 \tilde{Z}^2} \beta \tilde{Z} - m\beta \tilde{Z} \right. \\
&\qquad \left. -\gamma \frac{\beta^2 \tilde{Z}^2}{k^2 + \beta^2 \tilde{Z}^2} \right] \\
&= \frac{bg}{r} \tilde{Z}\left(\frac{c_p K^2 \tilde{P}^2 + c_z K^2 \tilde{Z}^2}{\mu^2 + c_p K^2 \tilde{P}^2 + c_z K^2 \tilde{Z}^2} \right) - \frac{g}{r}\tilde{Z}\left(\frac{c_z K^2 \tilde{Z}^2}{\mu^2 + c_p K^2 \tilde{P}^2 + c_z K^2 \tilde{Z}^2} \right) \\
&\qquad -\frac{m}{r}\tilde{Z} - \frac{\gamma}{r}\left(\frac{K\tilde{Z}^2}{k^2 + K^2 \tilde{Z}^2} \right) \\
&= \frac{bg}{r}\tilde{Z} \cdot \frac{\cancel{K^2}}{\cancel{K^2}}\left(\frac{c_p \tilde{P}^2 + c_z \tilde{Z}^2}{\frac{\mu^2}{K^2} + c_p \tilde{P}^2 + c_z \tilde{Z}^2} \right) - \frac{g}{r}\tilde{Z} \cdot \frac{\cancel{K^2}}{\cancel{K^2}}\left(\frac{c_z \tilde{Z}^2}{\frac{\mu^2}{K^2} + c_p \tilde{P}^2 + c_z \tilde{Z}^2} \right) \\
&\qquad -\frac{m}{r}\tilde{Z} - \frac{\gamma}{r}\frac{\cancel{K^2}}{\cancel{K^2}}\left(\frac{\frac{\tilde{Z}^2}{K}}{\frac{k^2}{K^2} + \tilde{Z}^2} \right).
\end{aligned}
$$

Using the same values for $f = \frac{g}{r}$ and $h^2 = \frac{\mu^2}{K^2}$, and setting $j = \frac{m}{r}$, $l = \frac{\gamma}{rK}$, and $q^2 = \frac{k^2}{K^2}$ (all the parameters are unitless), the final nondimensionalized version of the zooplankton equation is

$$
\begin{aligned}
\frac{d\tilde{Z}}{d\tilde{t}} &= bf\tilde{Z}\left(\frac{c_p \tilde{P}^2 + c_z \tilde{Z}^2}{h^2 + c_p \tilde{P}^2 + c_z \tilde{Z}^2} \right) - f\tilde{Z}\left(\frac{c_z \tilde{Z}^2}{h^2 + c_p \tilde{P}^2 + c_z \tilde{Z}^2} \right) - j\tilde{Z} \\
&\qquad -l\left(\frac{\tilde{Z}^2}{q^2 + \tilde{Z}^2} \right). \tag{B.2}
\end{aligned}
$$

If the prey choices are constant, they do not need to be nondimensionalized, as they are unitless. If instead the relative prey choice (c_p and c_z) are functions of P,

they also need to be nondimensionalized. Since $P = K\tilde{P}$ and $Z = K\tilde{Z}$:

$$c_z(\tilde{P}, \tilde{Z}) = \frac{1}{1 + (a\tilde{P}/\tilde{Z})^2} \tag{B.3}$$

since the K's from P and Z equations cancel out.

The third and final hypothesis is if the prey choices are dependent on a threshold of phytoplankton being met. Since $P = K\tilde{P}$:

$$c_z(\tilde{P}) = e^{-(\tilde{P}/\tilde{P}_0)^2}, \tag{B.4}$$

where $\tilde{P}_0 = P_0/K$.

B.2   P-Z-Z Model

Using the same technique and similar functions as the nondimensionalization of the P-Z model with cannibalism (see Appendix B.1), let $P = \alpha\tilde{P}$, $Z_0 = \beta\tilde{Z}_0$, $Z_1 = \Omega\tilde{Z}_1$ and $t = \tau\tilde{t}$. Then $d\tilde{P} = \frac{1}{\alpha}dP$, $d\tilde{Z}_0 = \frac{1}{\beta}dZ_0$, $d\tilde{Z}_1 = \frac{1}{\Omega}dZ_1$, and $d\tilde{t} = \frac{1}{\tau}dt$. Rates, constants, and variables K, k, μ, P, Z_0, and Z_1 have units of abundance. Rates g, r, and m have units of $\frac{1}{time}$. Rate γ has units of $\frac{abundance}{time}$. Finally, the constants d, b, c_p, and c_z are unitless.

First, nondimensionalize the first differential equation. Let $\alpha = K$, $\beta = K$, $\Omega = K$, and $\tau = \frac{1}{r}$:

$$
\begin{aligned}
\frac{d\tilde{P}}{d\tilde{t}} &= \frac{\tau}{\alpha}\frac{dP}{dt} = \frac{\tau}{\alpha}\left[r\alpha\tilde{P}\left(1 - \frac{\alpha\tilde{P}}{K}\right) - g\frac{\alpha\tilde{P}}{\mu + \alpha\tilde{P}}B\tilde{Z}_0 - g\frac{c_p\alpha^2\tilde{P}^2}{\mu^2 + c_p\alpha^2\tilde{P}^2 + c_z\beta^2\tilde{Z}_0^2}\Omega\tilde{Z}_1\right] \\
&= \tilde{P}(1 - \tilde{P}) - \frac{gK\tilde{Z}_0}{r}\frac{\cancel{K}}{\cancel{K}}\left(\frac{\frac{\tilde{P}}{K}}{\frac{\mu}{K} + \tilde{P}}\right) - \frac{g\Omega\tilde{Z}_1}{r}\frac{\cancel{K^2}}{\cancel{K^2}}\left(\frac{\frac{c_p\tilde{P}^2}{K}}{\frac{\mu^2}{K^2} + c_p\tilde{P}^2 + c_z\tilde{Z}_0^2}\right).
\end{aligned}
$$

Choosing nondimensionalized unitless functions of temperature, let $f = \frac{g}{r}$ and $h = \frac{\mu}{K}$. Therefore, the final nondimensionalized version of the phytoplankton differential equation is

$$\frac{d\tilde{P}}{d\tilde{t}} = \tilde{P}(1 - \tilde{P}) - f\tilde{Z}_0\frac{\tilde{P}}{h + \tilde{P}} - f\tilde{Z}_1\frac{c_p\tilde{P}^2}{h^2 + c_p\tilde{P}^2 + c_z\tilde{Z}_0^2}. \tag{B.5}$$

Nondimensionalize the second differential equation and use the same values for $\tilde{P}$, $\tilde{Z}_0$, $\tilde{Z}_1$, and $\tilde{t}$, and let $\tau = \frac{1}{r}$, $\alpha = \beta = \Omega = K$, and $f = \frac{g}{r}$ and $h = \frac{\mu}{K}$:

$$
\begin{aligned}
\frac{d\tilde{Z}_0}{d\tilde{t}} &= \frac{\tau}{\beta}\left[g\frac{bc_p\alpha^2\tilde{P}^2 + (b-1)c_z\beta^2\tilde{Z}_0{}^2}{\mu^2 + c_p\alpha^2\tilde{P}^2 + c_z\beta^2\tilde{Z}_0{}^2}\Omega\tilde{Z}_1 - dg\frac{\alpha\tilde{P}}{\mu + \alpha\tilde{P}}\beta\tilde{Z}_0 - m\beta\tilde{Z}_0\right.\\
&\qquad\left. -\gamma\frac{\beta^2\tilde{Z}_0{}^2}{k^2 + \beta^2\tilde{Z}_0{}^2 + \beta^2\tilde{Z}_1{}^2}\right]\\
&= \frac{g}{r}\tilde{Z}_1\frac{\cancel{K^2}}{\cancel{K^2}}\left(\frac{bc_p\tilde{P}^2 + (b-1)c_zK^2\tilde{Z}_0{}^2}{\frac{\mu^2}{K^2} + c_p\tilde{P}^2 + c_z\tilde{Z}_0{}^2}\right) - \frac{dg}{r}\tilde{Z}_0\frac{\cancel{K}}{\cancel{K}}\left(\frac{\tilde{P}}{\frac{\mu}{K} + \tilde{P}}\right) - \frac{m\tilde{Z}_0}{r}\\
&\qquad -\frac{\gamma}{rK}\frac{\cancel{K^2}}{\cancel{K^2}}\left(\frac{\tilde{Z}_0{}^2}{\frac{k^2}{K^2} + \tilde{Z}_0{}^2 + \tilde{Z}_1{}^2}\right).
\end{aligned}
$$

Letting $j = \frac{m}{r}$, $l = \frac{\gamma}{rK}$, and $q = \frac{k}{K}$, the final nondimensionalized version of the immature zooplankton differential equation is

$$
\frac{d\tilde{Z}_0}{d\tilde{t}} = f\tilde{Z}_1\frac{b_cp\tilde{P}^2 + (b-1)c_z\tilde{Z}_0{}^2}{h^2 + c_p\tilde{P}^2 + c_z\tilde{Z}_0{}^2} - df\tilde{Z}_0\frac{\tilde{P}}{h + \tilde{P}} - j\tilde{Z}_0 - l\frac{\tilde{Z}_0{}^2}{q^2 + \tilde{Z}_0{}^2 + \tilde{Z}_1{}^2}. \quad \text{(B.6)}
$$

Nondimensionalize the third differential equation and use the same values for $\tilde{P}$, $\tilde{Z}_0$, $\tilde{Z}_1$, and $\tilde{t}$, and let $\tau = \frac{1}{r}$, $\alpha = \beta = \Omega = K$, and $f = \frac{g}{r}$, $h = \frac{\mu}{K}$, $j = \frac{m}{r}$, $l = \frac{\gamma}{rK}$, and $q = \frac{k}{K}$:

$$
\begin{aligned}
\frac{d\tilde{Z}_1}{d\tilde{t}} &= \frac{\tau}{\Omega}\frac{dZ_1}{dt} = \frac{\tau}{\Omega}\left[dg\frac{\alpha\tilde{P}}{\mu + \alpha\tilde{P}}b\tilde{Z}_0 - m\Omega\tilde{Z}_1 - \gamma\frac{\Omega^2\tilde{Z}_1{}^2}{k^2 + \beta^2\tilde{Z}_0{}^2 + \Omega^2\tilde{Z}_1{}^2}\right]\\
&= \frac{dg}{r}\frac{\cancel{K}}{\cancel{K}}\frac{\tilde{P}}{\frac{\mu}{K} + \tilde{P}}\tilde{Z}_0 - \frac{m}{r}\tilde{Z}_1 - \frac{\gamma}{rK}\frac{\cancel{K^2}}{\cancel{K^2}}\frac{\tilde{Z}_1{}^2}{\frac{k^2}{K^2} + \tilde{Z}_0{}^2 + \tilde{Z}_1{}^2}.
\end{aligned}
$$

Therefore, the final nondimensionalized version of the mature zooplankton differential equation is

$$
\frac{d\tilde{Z}_1}{d\tilde{t}} = df\frac{\tilde{P}}{h + \tilde{P}}\tilde{Z}_0 - j\tilde{Z}_1 - l\frac{\tilde{Z}_1{}^2}{q^2 + \tilde{Z}_0{}^2 + \tilde{Z}_1{}^2}. \quad \text{(B.7)}
$$