

A Dynamical Systems Approach to Modeling
Plankton Food Chains

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1 Abstract

The main focus of this project is modeling phytoplankton predator-prey systems involving a resource, a prey (phytoplankton), and a predator (zooplankton) in order to understand the complex interactions between these constituents. It is important to study food chains, because phytoplankton contribute to numerous biogeochemical processes in nature. For example they control water quality, influence the global climate by regulating the carbon dioxide uptake, and form the base for most aquatic food chains. Because phytoplankton are simple and small organisms with short life spans, they are relatively easy to study. Lab and field experiments can be readily combined with theoretical analyses.

In this paper we first investigate simple cases involving a resource and one to two phytoplankton species both within and outside a chemostat and then turn our attention to more complex ones consisting of all three components. Some models include mathematically convenient approximations for fluctuations in resource availability and seasonal variations. We employ a dynamical systems approach and supporting numerical simulations to study both short-term and long-term behavior. Our findings show that for long periods under forcing distinct regimes of species coexistence that can be analytically computed are present. Also, as the total nutrient content is varied, the system with all three components undergoes several bifurcations, resulting in drastic, dynamical changes ranging from coexistence of both species to dominance of just zooplankton or extinction of both. Future research will concentrate on incorporating more realistic functional responses, seasonal transitions, and time periods.

2 Introduction

Phytoplankton contribute to numerous biogeochemical processes and constitute the basis for most aquatic food chains. They play an essential role in controlling the water quality and exert a great influence on the global climate by regulating carbon dioxide (CO_2) uptake.³ Moreover, changes in phytoplankton population can alert scientists to alterations in the environment. Phytoplankton can also be useful in determining where ocean currents provide nutrients for plant growth and where pollutants poison the ocean and prevent plant growth.² Because phytoplankton are small, elementary creatures with short life spans, their dynamics are relatively easy to model. In addition, laboratory and field experiments are feasible.^{4,6}

Phytoplankton require only a few things to survive: sunlight, water, and nutrients. Chlorophyll allows phytoplankton to utilize light energy, which is used to fix CO_2 to sugars and generate ATP.⁷ Oxygen is then released as a byproduct. Essential nutrients include CO_2 , nitrogen, sulfur, phosphorus compounds, Si, Fe, and other trace metals. Some species of phytoplankton also require vitamins like thiamin or biotin to survive.⁴

The rest of this paper is organized as follows. At first, we consider simple systems that include a resource and one or two phytoplankton within as well as outside a chemostat. Subsequently, we examine more complex models that include seasonal variations in resource availability. The main question of this research effort is how does seasonal forcing affect system dynamics.

3 One Phytoplankton Species in Chemostat with One Limiting Nutrient

In this section, we investigate a resource-consumer system in a chemostat, in which, a nutrient solution is pumped into a reservoir containing phytoplankton. A mixture of nutrient and phytoplankton is pumped out at the same rate. The equations governing the model with only one phytoplankton in a chemostat and one limiting nutrient are¹

$$\begin{aligned}\frac{dR}{dt} &= a(R_{\text{in}} - R) - f(R)P \\ \frac{dP}{dt} &= yf(R)P - mP,\end{aligned}\tag{1}$$

where P is the population size of the phytoplankton, R is the concentration of the limiting nutrient remaining in the solution, and R_{in} is the amount of resource pumped into the system. The nutrient yield from the resource consumption is denoted by y and the flow rate at which the solution is pumped is given experimentally and denoted by a . It, of course, has to be restricted because the entire culture would be washed out at large a .¹ Biomass is lost at a rate m ($m > a$) and the growth rate is given by the Monod consumption function¹

$$f(R) = \frac{vR}{R + k},\tag{2}$$

where k is the half-saturation constant and v is the maximum intake of resources by the phytoplankton (see Fig. 1). This type of functional response is called type II: For low resource level, the response is linear (as phytoplankton are capable of consuming all of the resources that are available), but the ability to consume the resource saturates as the resource availability

increases (as expected biologically).

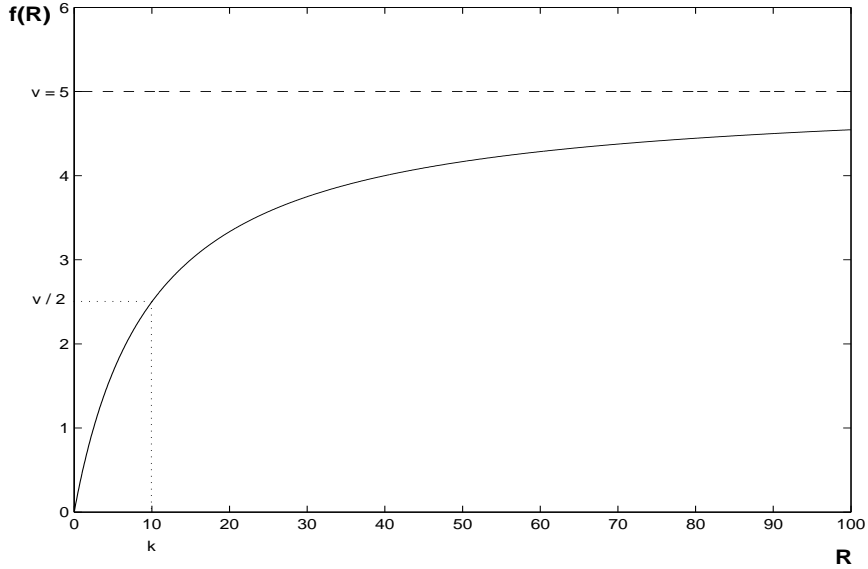


Figure 1: The Monod (type II) consumption functional response $f(R)$ as resources R vary. (The parameter k is the half-saturation constant and v is the maximum resource intake.)

For a single species to persist, it must be able to invade the empty system.⁶ (This is called the "invasibility criterion.") The phytoplankton will grow as long as there are enough nutrients for them to consume. Let R^* denote the minimum amount of nutrient that the phytoplankton species needs to survive. By setting $\frac{1}{P} \frac{dP}{dt} = 0$, one finds that $R^* = km/(vy - m)$. The system's equilibria are found using its nullclines. To determine stability, the Jacobian needs to be evaluated at each equilibrium and its eigenvalues need to be computed. This system has two equilibria, the first of which is $(\hat{P}, \hat{Z}) = (0, R_{\text{in}})$ corresponding to no biomass ("hat" indicates an equilibrium value). If $R_{\text{in}} < R^*$, then this equilibrium is a sink, so there are insufficient resources

for the system to be sustained and the species dies off. If $R_{in} > R^*$, this equilibrium is a saddle point (unstable). The second equilibrium, a spiral sink, is biologically relevant only when $P > 0$. The phase portrait with arrows indicating the dynamics of the system in each region is shown in Fig. 2.

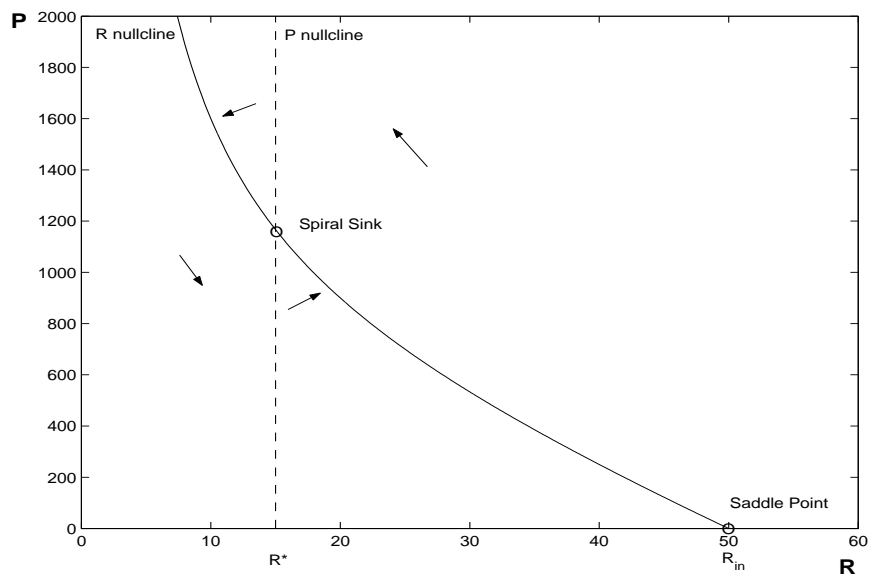


Figure 2: Phase plane P vs. R for $R_{in} > R^*$. The two equilibria are a saddle point and a spiral sink. The arrows indicate the flow of the vector field at the indicated point.

4 Two Phytoplankton Species in Chemostat with One Limiting Nutrient

In this section, we examine chemostats with two competing phytoplankton species. The following set of differential equations describes the dynamics in the presence of a single nutrient:⁵

$$\begin{aligned}\frac{dR}{dt} &= a(R - R_{\text{in}}) - f_1(R)P_1 - f_2(R)P_2 \\ \frac{dP_1}{dt} &= y_1 f_1(R)P_1 - m_1 P_1 \\ \frac{dP_2}{dt} &= y_2 f_2(R)P_2 - m_2 P_2.\end{aligned}\tag{3}$$

This system has three equilibria, each of which includes one resource per living species. These occur at $(R_{\text{in}}, 0, 0)$, $(R_1^*, y_1 a(R_{\text{in}} - R_1^*)/m_1, 0)$, and $(R_2^*, 0, y_2 a(R_{\text{in}} - R_2^*)/m_2)$, where R_1^* and R_2^* are defined in the same fashion as for one species (see section 3).

The two species of phytoplankton have no direct effect on each other; they interact only by limiting resource availability. Here, R^* is a measure of competitive ability (see Fig. 3). The species with lower R^* outlives the other. In his seminal work,⁴ Hutchinson coined the term “paradox of the plankton” to describe this phenomenon. He showed theoretically that the number of coexisting phytoplankton species at equilibrium is limited by the number of resources available, which in this case means that only one phytoplankton species should survive.⁸ However, in real world there are more species than nutrients so some of the assumptions do not hold. In fact, if each species can invade a monoculture of the other, long-term stable co-existence can occur, if neither species can, then the outcome of competition depends on initial

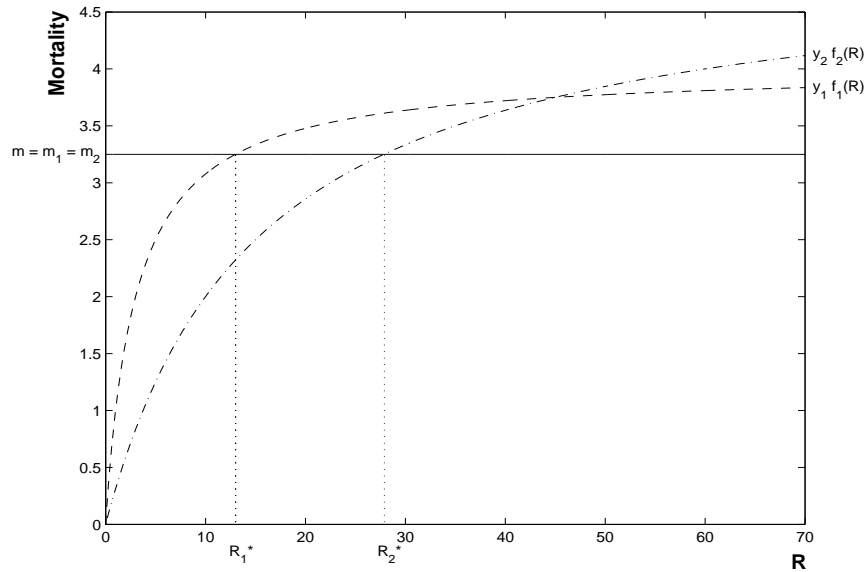


Figure 3: Functional responses for two species in a chemostat for $m_1 = m_2$, where R_j^* represents the minimum amount of resources needed for survival of species j . It is evident that species 1 should prevail at equilibrium in this particular situation.

conditions.⁶

5 Generalized Predator-Prey System

In this section, we consider a model that allows a living, reproducing resource,

$$\begin{aligned} \frac{dR}{dt} &= rR \left(1 - \frac{R}{c}\right) - f(R)P \\ \frac{dP}{dt} &= yf(R)P - mP, \end{aligned} \tag{4}$$

where R is the population size of the prey and P is the population size of the predator. The logistic form of the first term in the expression for dR/dt reflects the behavior of prey in the absence of predation. The parameter r represents the maximum per capita growth rate and c is the carrying capacity (i.e., the maximum prey population that the environment can support). In addition, y is the yield of predators from each prey and m is the predator's mortality rate. The functional response is given in equation (2). Recall that k is the half-saturation constant and v is the maximum intake of resources by the predator. Equilibria occur at $(0, 0)$, $(c, 0)$, and $(R^*, [r/v][1 - R^*/c][R^* + k])$. Predators die off at the trivial equilibrium. When $c < R^*$, the second equilibrium is a sink, so the system cannot sustain a population of prey large enough for survival. The third equilibrium is biologically irrelevant, as the population cannot be negative. For $c > R^*$, $(c, 0)$ becomes an unstable saddle point, whereas the stability of $(R^*, [r/v][1 - R^*/c][R^* + k])$ depends on the magnitude of c . For substantially larger values of c , the equilibrium becomes unstable, while for values of c just slightly above R^* , it is a sink. Determining the exact value for c , at which the qualitative equilibrium behavior changes, is complicated. "Nondimensionalizing" equation (4) reveals the relevant parameter combinations necessary to understand the governing dynamics of this model. The resulting substitutions are

$$\begin{aligned}
 R' &= \frac{R}{c} & t' &= rt & P' &= \frac{P}{yc} \\
 k_1 &= \frac{yv}{r} & k_2 &= \frac{k}{c} & k_3 &= \frac{m}{r},
 \end{aligned} \tag{5}$$

Dropping the primes, equation (4) becomes

$$\begin{aligned}\frac{dR}{dt} &= R(1 - R) - \frac{k_1 RP}{R + k_2} \\ \frac{dP}{dt} &= \frac{k_1 RP}{R + k_2} - k_3 P.\end{aligned}\tag{6}$$

The equilibria now occur at $(0, 0)$, $(1, 0)$, and $(R^*, [1 - R^*][R^* + k_2]/k_1)$, where R^* is computed from the rescaled functional response. In this case, the second equilibrium is a stable sink if $R^* > 1$ and a saddle point if R^* is below 1. The third equilibrium point is unstable, when $k_2 \in [0, (k_1 - k_3)/(k_1 + k_3)]$. For small values of k_2 extremely wide limit cycles that are very close to the axis are present, which for a real system with discrete populations means extinction of either predator or prey or both. The third equilibrium becomes a stable spiral sink when $k_2 \in [(k_1 - k_3)/(k_1 + k_3), (k_1 - k_3)/k_3]$, and is not biologically applicable if $k_2 > (k_1 - k_3)/k_3$. The first threshold value for k_2 translates into an original threshold value for c of $R^*(1 + yv/m)$. The phase portrait for the system is presented in Fig. 4.

6 Seasonal Forcing in a Phytoplankton Food Chain

Most models don't include seasonal succession, or periodic resetting of system dynamics, and resource variations. Seasonal forcing is necessary to better characterize phytoplankton development, because of the changing physical environment. In the spring, light is a limiting resource for the phytoplankton in a lake. The water is warming and even mixing due to the lake's wind and water currents. However, in the beginning stages of summer, when

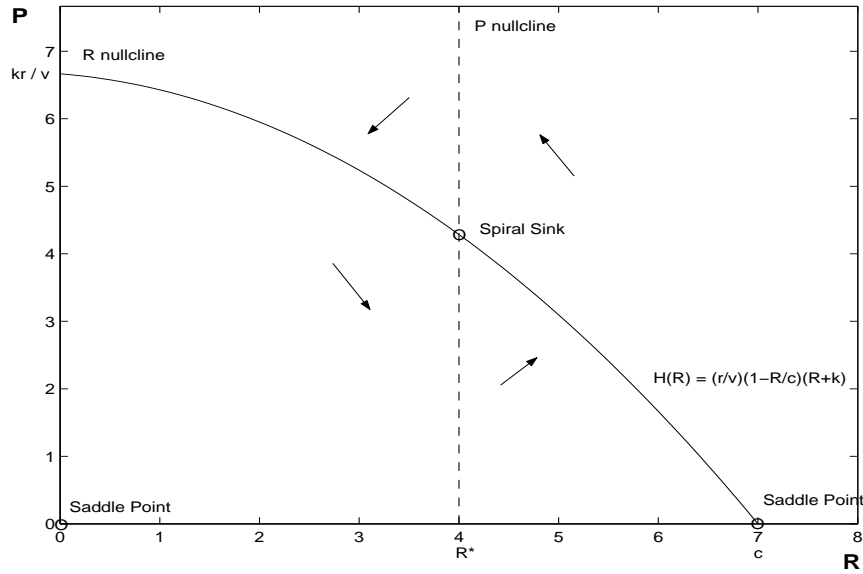


Figure 4: Phase plane P vs. R for parameter $c \in [R^*, R^*(1 + yv/m)]$. The three equilibria are a saddle point at the origin, a spiral sink at $(R^*, H(R^*))$, and a saddle point at $(c, 0)$.

the phytoplankton start to grow, mixing occurs mostly in two segments: the epilimnion, or warm layer of the lake, and the hypolimnion, or cold layer of the lake. There is also limited mixing between layers. Later in the summer, the nutrients become limited due to a now-large biomass of phytoplankton and – as the epilimnion and the hypolimnion approach the same temperature – there is greater mixing between layers. As the water temperature increases during the fall overturn, phytoplankton get pulled to the bottom when colder water sinks and nutrients rise to the surface. Once the phytoplankton reach the bottom, cold layer of the lake, it becomes almost impossible for the phytoplankton to resurface, where they can obtain enough light and nutrients to survive. Thus, most phytoplankton die off in the fall overturn.

Periodic forcing can be modeled mathematically by having one equation for the growing season and a separate one for the dying season. We again nondimensionalize the system, so that the total season has unit period. In our model, the growing season lasts a proportion p of the time and is governed by the following dynamical system:

$$\begin{aligned}\frac{dP}{dt} &= T(c_1RP - m_pP - c_2PZ) \\ \frac{dZ}{dt} &= T(c_3PZ - m_zZ).\end{aligned}\tag{7}$$

During the remainder of the dying season, when $t \in [p, 1]$, there are no resources, which yields the governing dynamical system:

$$\begin{aligned}\frac{dP}{dt} &= T(-m_pP - c_2PZ) \\ \frac{dZ}{dt} &= T(c_3PZ - m_zZ).\end{aligned}\tag{8}$$

Both sets of equations incorporate a type I, (i.e., linear), functional response. In our case, it is given by $f_P(R) = c_1R$ for phytoplankton and by $f_Z(P) = c_3P$ for zooplankton. The parameter R is the amount of nutrient, P is the nutrient content of phytoplankton, and Z is the nutrient content of zooplankton. The mortality rates of the phytoplankton and the zooplankton are given by m_p and m_z , respectively, and T represents the period. The parameter c_1 is the phytoplankton's nutrient yield from consuming resources, c_2 accounts for losses in phytoplankton population caused by zooplankton consumption, and c_3 is the zooplankton's nutrient yield from consuming phytoplankton. Clearly, c_3 cannot exceed c_2 . Otherwise, zooplankton would be receiving more nutrients from the phytoplankton than the phytoplankton are able to hold and additional biomass would be created

from nothing. In this closed system, the amount of total resources remains constant: $R_{\text{total}} = R + P + Z$. Depending on the parameter R_{total} , various dynamical regimes are possible; the system can either exhibit stable coexistence of both species at the end of the season (as illustrated in Fig. 5), annihilation of zooplankton and prevalence of phytoplankton, or extinction of both species.

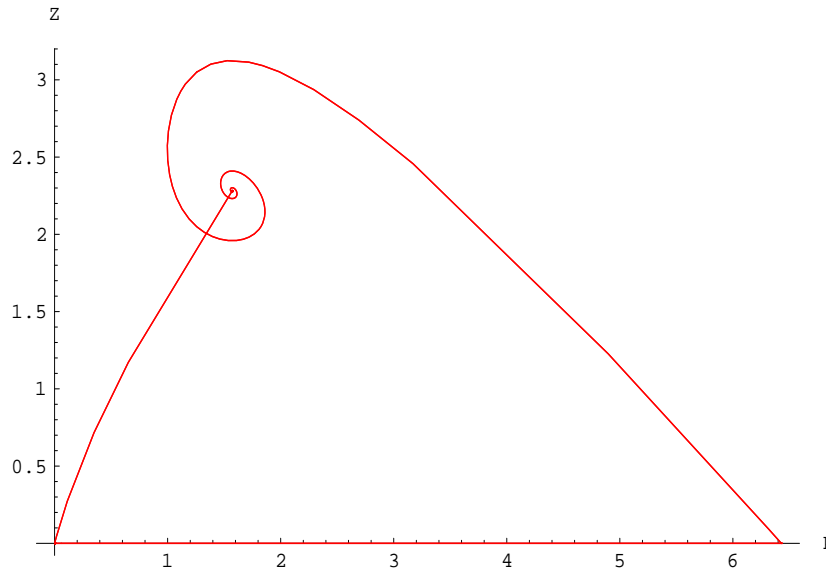


Figure 5: Phase plane of Z vs. P for large R_{total} . After $t = t_1$ the system jumps to $(\hat{P}, 0)$. After $t = t_2$ it ends up at (\hat{P}, \hat{Z}) . Finally, at time $t = p$, it returns to the origin.

In the long-term dying phase, $(\hat{P}, \hat{Z}) = (0, 0)$. This is sensible biologically, as the phytoplankton have nothing to eat and their population eventually declines, causing the zooplankton population to die out as well. During the time interval $[0, p]$, the system has three equilibria for $R_{\text{total}} > R^* + P^*$, as indicated in the bifurcation diagram in Fig. 6; these are $(0, 0)$, $(\hat{P}, 0)$, and

(\hat{P}, \hat{Z}) . At $(0, 0)$, all species are dead; this is a stable sink. The equilibrium at $(\hat{P}, 0)$ indicates that the zooplankton have completely died off and $\frac{dP}{dt} = 0$. It is evident that $\hat{P} = R_{\text{total}} - R^*$, where $R^* = m_p/c_1$. Both species coexist at (\hat{P}, \hat{Z}) . One finds that $\hat{P} = P^* = m_z/c_3$. Upon substitution, we obtain $\hat{Z} = (c_1(R_{\text{total}} - P^*) - m_p)/(c_1 + c_2)$.

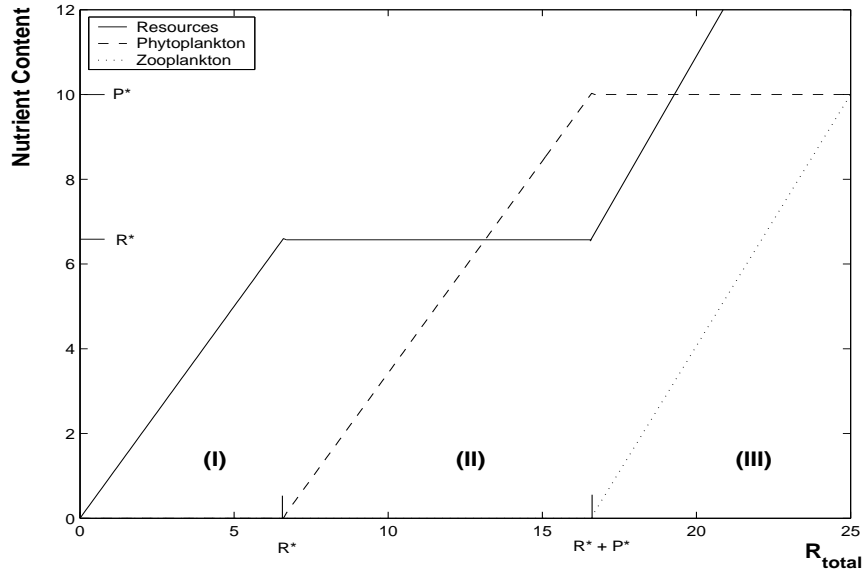


Figure 6: Bifurcation diagram for the parameter R_{total} . Three regimes are possible: phytoplankton and zooplankton both coexist (I), phytoplankton prevail (II), or neither lives (III).

As indicated by the numerical simulations for long periods (see Fig. 7), there exists a time t_1 such that during the time interval $[0, t_1]$, both species are near zero. Immediately thereafter, a stable population of phytoplankton emerges and prevails during the time interval $[t_1, t_2]$. From then until the end of the growing season, $t \in [t_2, p]$, both species coexist. Right after the resources are fully consumed, both populations rapidly decline to zero; this

occurs in the time period $[p, 1]$.

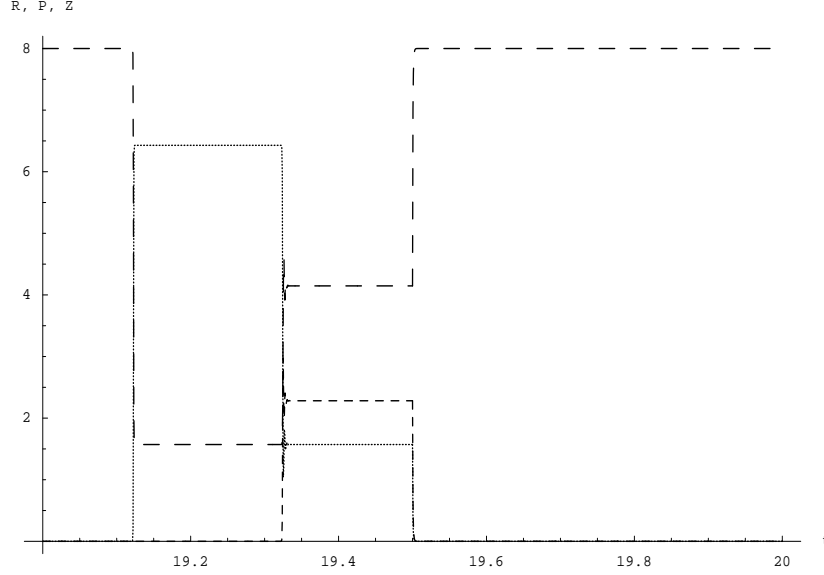


Figure 7: Long-term numerical simulation with period $T = 1250$, $R_{\text{total}} = 8$, $p = 0.5$, $c_1 = 0.7$, $c_2 = 0.79$, $c_3 = 0.7$, $m_p = 1.1$, and $m_z = 1.1$. For $t \in [0, t_1]$ both species are near zero; when $t \in [t_1, t_2]$, a stable population of phytoplankton emerges and prevails; $t \in [t_2, p]$ – both species coexist; $t \in [p, 1]$ – both populations rapidly decline to zero.

The two times t_1 and t_2 can be found using linearization and the fact that the per capita rate of change averaged over the whole period must vanish: $\int_0^1 \frac{P'}{P} d\tau = \int_0^1 \frac{Z'}{Z} d\tau = 0$. Each integral is then split into four distinct phases:

$$\begin{aligned} \int_0^1 \frac{P'}{P} d\tau &= \int_0^{t_1} \frac{P'}{P} d\tau + \int_{t_1}^{t_2} \frac{P'}{P} d\tau + \int_{t_2}^p \frac{P'}{P} d\tau + \int_p^1 \frac{P'}{P} d\tau = 0 \\ \int_0^1 \frac{Z'}{Z} d\tau &= \int_0^{t_1} \frac{Z'}{Z} d\tau + \int_{t_1}^{t_2} \frac{Z'}{Z} d\tau + \int_{t_2}^p \frac{Z'}{Z} d\tau + \int_p^1 \frac{Z'}{Z} d\tau = 0. \end{aligned}$$

Using linearization, these equations become

$$\int_0^{t_1} (c_1 R_{\text{total}} - m_p) d\tau + \int_{t_1}^{t_2} (0) d\tau + \int_{t_2}^p (0) d\tau + \int_p^1 (-m_p) d\tau = 0$$

$$\int_0^{t_1} (-m_z) d\tau + \int_{t_1}^{t_2} (c_3(R_{\text{total}} - \frac{m_p}{c_1}) - m_z) d\tau + \int_{t_2}^p (0) d\tau + \int_p^1 (-m_z) d\tau = 0$$

Performing the integrals and solving the linear system, it follows that:

$$t_1 = \frac{(1-p)m_p}{c_1 R_{\text{total}} - m_p} \quad , \quad t_2 = \frac{m_z(1-p) + c_3(R_{\text{total}} - m_p/c_1)t_1}{c_3(R_{\text{total}} - m_p/c_1) - m_z}.$$

Note that there are no zooplankton parameters present in the expression for t_1 .

7 Conclusions

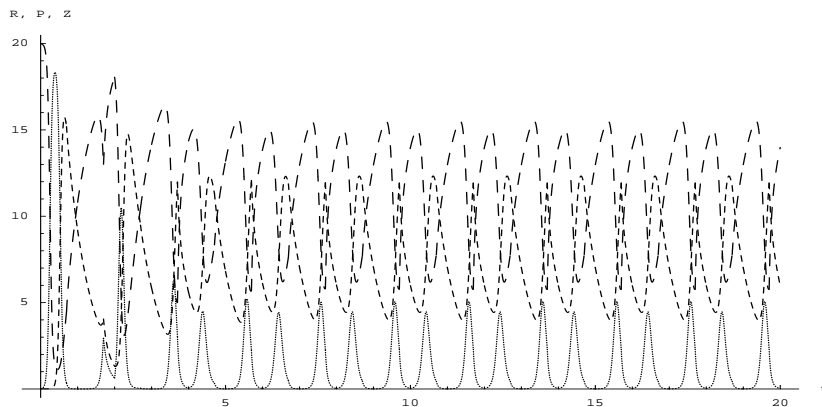


Figure 8: Short period ($T = 2$) numerical simulation showing 20 periods that form “clusters” of 2 (excluding the first few “transient” periods). Phytoplankton (\cdot), zooplankton ($-$), resources (\cdot).

Regular, autonomous predator-prey food webs with just a resource and few phytoplankton are readily examined using standard mathematical techniques for systems of differential equations. Analytical results for and near equilibria are possible. The main concern of this research is the effects of seasonal forcing on system dynamics. More involved food chains consist of all

three components and account for seasonal resource fluctuations. Both our analytical and numerical findings reveal that for long periods under seasonal forcing distinct regions of species coexistence are present and are similar to those without the seasonal forcing. For shorter periods these approximations become unreasonable and different methods are needed. Also, the system's total nutrient content plays a vital role in its aggregate dynamics - several bifurcations are present as this parameter is varied, causing severe changes in system's behavior: from coexistence of both species to extinction of phytoplankton to disappearance of both.

We are continuing this research during the fall 2004 semester. Seasonal succession is constant only in the long-term when the system is free of perturbations. We plan to investigate the behaviors of various systems for smaller periods, where seasons might not be identical but rather form periodic clusters, using multiple-scale perturbation theory (see Fig. 8). We hope to examine seasonally forced systems with a more realistic type II, saturated exponential, functional response, as well. In nature, resource switching never occurs instantaneously. Rather, the transition occurs during a comparatively short time. We want to incorporate this more realistic approach into the model using, for example, an exponential saturated transition. We also hope to get an insight on ecologically interesting "diamond" food webs (that are not understood well) that include two phytoplankton species, a zooplankton species that feeds on them, and a common base resource.

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