A Dynamical Systems Approach to Modeling Plankton Food Web

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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 predators (zooplankton) in order to understand the complex interactions between these constituents. It is important to study these food chains, because phytoplankton contribute to numerous biogeochemical processes in nature. They control water quality, influence global climate by regulating carbon dioxide uptake, and form the basis 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 experiments can be readily combined with theoretical analyses.

In this paper, we first investigate a food web consisting of a chain of a single zooplankton feeding on a phytoplankton which is dependent on a resouce. The model includes mathematically convenient approximation for the fluctuation in resource availability and seasonal variations. We employ a dynamical systems approach and supporting numerical simulations to study long-term behavior. Our findings show that for long periods under forcing, distinct regimes of species coexistence are present and can be analytically computed. As the total nutrient content is varied, the system undergoes several bifurcations, resulting in drastic, dynamical changes ranging from coexistence of both species to dominance of only zooplankton to extinction of both. A smooth seasonal transition, convenient for analytics, was also introduced allowing for the decline of resources not to be abrupt. A food web consisting of a resource, a phytoplankton, and two zooplankton species competing for a single phytoplankton was also investigated. Most combina-

tions of parameters result in the dominance of one species of the zooplankton with total extinction of the other, which reduces to the first case examined. Using a type II functional response and considering only a narrow parameter subset, one is able to observe some interesting dynamics when switching of zooplankton dominance occurs. We found that the length of the growing season is directly involved in the system dynamics. The length of the growing season can be too short for the phytoplankton or the fast growing zooplankton to emerge or it can be long enough for the good competitor zooplankton to dominate.

2   Introduction

Phytoplankton contribute to numerous biogeochemical processes and constitute the basis for most aquatic food chains. They play an essential role in controlling 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.[4,5]

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.[6] 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]

Predator-prey models help forecast population trends and disease outbreaks. They can also aid in the understanding of biological community structure. The most basic kind of food chain involves a prey species feeding off a nutrient. This can be generated to more complex models that include species interactions. The first predator-prey model was formulated by Lotka and Volterra. The Lotka-Volterra system consists of one predator species and one prey species. Lotka-Volterra assumes the predator is completely dependent on the prey for its food supply and that the size of the prey population is restricted only by predation. This model shows that predators and prey can coexist, in that both species follow stable cycle oscillations. Rosenzweig and MacArthur expanded this model further to include consumption rates of predators.[1]

Most predator-prey models do not 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 occurs due to the lake's wind and water currents. However, in the beginning stages of summer, when the phytoplankton start to grow, mixing occurs mostly in two sections: the epilimnion, or warm layer of the lake, and the hypolimnion, or cold layer of the lake. There is also limited mixing betweeen layers. Later in the summer, the nutrients become limited due to the 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, and can obtain enough light and nutrients to survive. Thus, most phytoplankton die off in the fall overturn.

The main question of this research effort is how does seasonal forcing or, more specifically, the length of the growing season affect system dynamics. The rest of this paper is organized as follows. First, we consider a system that includes a resource, one phytoplankton, and one zooplankton with seasonal variation in resource availability. Subsequently, we examine a more complex model that includes a resource, one phytoplankton, and two zooplankton.

3 Seasonal Forcing in a Phytoplankton Food Chain with One Zooplankton Species

Periodic forcing can modeled mathematically by having one equation for the growing season and a separate one for the dying season and assuming that the duration of the growing season is the same each year. We 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:

$$\frac{dP}{dt} = T(c_1 PR - m_p P - f_p(R)Z)$$
$$\frac{dZ}{dt} = T(f_z(P)P - m_z Z).$$

(1)

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

$$\frac{dP}{dt} = T(-m_p P - f_p(R)Z)$$
$$\frac{dZ}{dt} = T(f_z(P)P - m_z Z).$$

(2)

The functional response represents the per capita rate of prey consumed in unit time.[1] Functional responses are either linear (type I) or saturating (type II). In this model, both sets of equations incorporate a type I functional response in which the predator consumption rate increases with prey density until reaching a maximum consumption rate. This is written mathematically as $f_P(R) = c_2 P$ for phytoplankton and $f_Z(P) = c_3 Z$ 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, $c_3 \leq c_2$; otherwise, zooplankton would receive more nutrients from the phytoplankton than the phytoplankton are able to hold and additional biomass would be created from nothing. Because this system is closed, the

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amount of total resources remains constant: $R_{\text{tot}} = R + P + Z$. Depending on the parameter R_{tot}, 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. 1), annihilation of zooplankton and prevalence of phytoplankton, or extinction of both species.
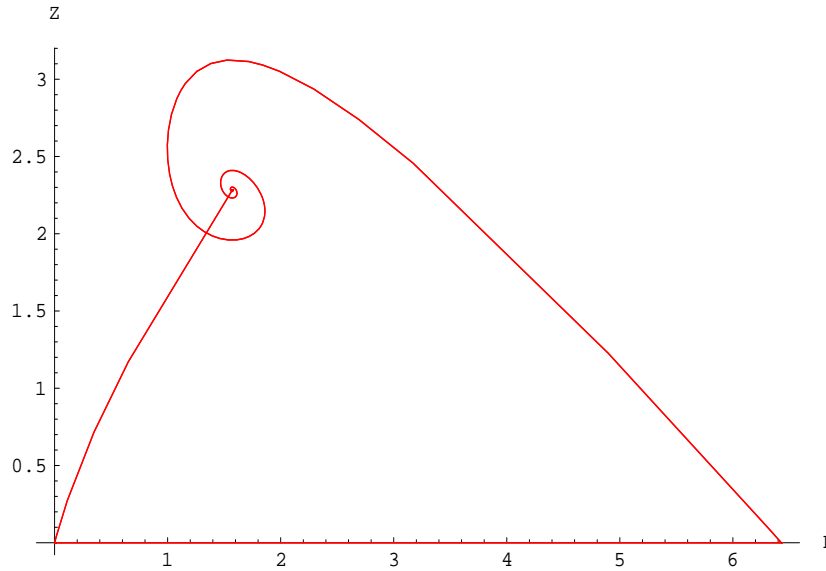

Figure 1: Phase plane of Z vs. P for large R_{tot}. After $t = t_1$ the system jumps to $(\hat{P}, 0)$. After $t = t_2$ it ends up at $(\hat{P}, \hat{Z})$. Finally, at time $t = p$, it returns to the origin.

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 $R_{\text{tot}} > R^\star + P^\star$, as indicated in the bifurcation diagram in Fig. 2; 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

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at $(\hat{P}, 0)$ indicates that the zooplankton have completely died off and $\frac{dP}{dt} = 0$. It is evident that $\hat{P} = R_{\text{tot}} - R^\star$, where $R^\star = m_p/c_1$. Both species coexist at $(\hat{P}, \hat{Z})$. One finds that $\hat{P} = P^\star = m_z/c_3$. Upon substitution, we obtain $\hat{Z} = (c_1(R_{\text{tot}} - P^\star) - m_p)/(c_1 + c_2)$.
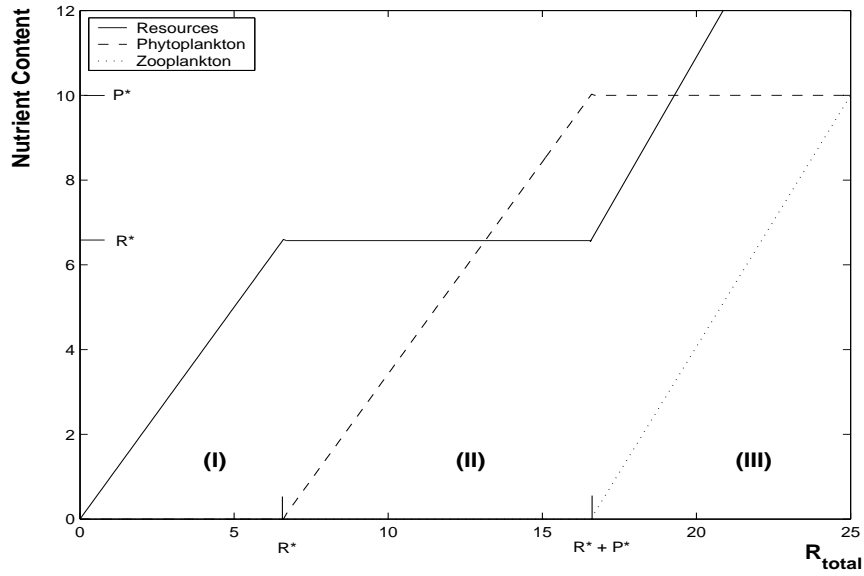

Figure 2: Bifurcation diagram for the parameter R_{tot}. Three regimes are possible: phytoplankton and zooplankton both coexist (I), phytoplankton prevail (II), or neither lives (III).

As indicated by the numerical simulations for long periods (see Fig. 3), 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 (i.e. for $t \in [t_2, p]$), both species coexist. Right after the resources are fully consumed, both populations rapidly decline to zero; this occurs in the time period $[p, 1]$.
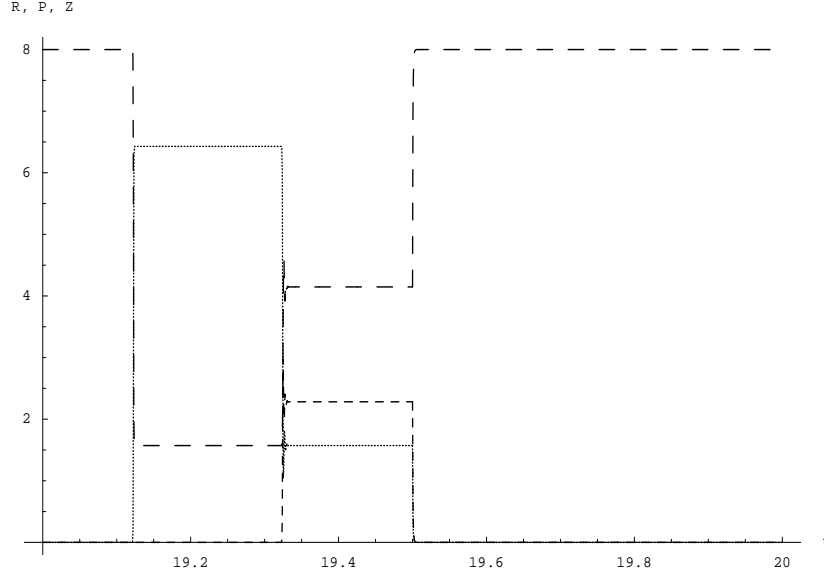
Figure 3: Long-term numerical simulation with period $T = 1250, R_{\text{tot}} = 8, p = 0.5, c_1 = 0.7, c_2 = 0.79, c_3 = 0.7, m_p = 1.1$, and $m_z = 1.1$. The long-dashed line indicates the resource, the dotted line respresents the phytoplankton, and the short-dashed line respresents zooplankton. For $t \in [0, t_1]$ 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.

We find the two times t_1 and t_2 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:

$$\int_0^1 \frac{P'}{P} d\tau = \int_0^{t_1} \frac{P'}{P} d\tau + \int_{t_1}^{t_2} \frac{P'}{P} d\tau + \int_{t_2}^{p} \frac{P'}{P} d\tau + \int_p^1 \frac{P'}{P} d\tau = 0$$

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

Using linearization, these equations become

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

Performing the integrals and solving the linear system gives the times

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

Because there are no zooplankton parameters present in the expression for t_1, it follows that the emergence of the phytoplankton is independent of the zooplankton population. This is consistent with the fact that there are negligibly many zooplantkon initially, so their population does not play a role in the dynamics.

If the discontinuous nature of the equations prevents analytical manipulations, then one can introduce smooth approximations so that the factors describing resources availability decreases sharply to zero immediately after time p. Two suitable candidates are: $-\frac{tan^{-1}(1000(t-p)) + \pi/2}{\pi}$ and $1 - \frac{e^{1000(t-p)}}{1 + e^{1000(t-p)}}$. Numerical simulations with both of these attenuation factors yield similar results to those we observed with the discontinuous case.

4   Seasonal Forcing in a Phytoplankton Food Web with Two Zooplankton Species

This system differs from the one described above by an addition of a second zooplankton species. Various system dynamics developments are summarized in figure 4.
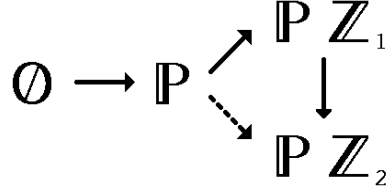
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Figure 4: Transitions diagram. The system can transition from the empty state into the state where only P exists. From the P state, either Z_i can invade. If the fast grower emerges first, then the good competitor can still invade the system.

The growing season (lasting proportion p of the period) is governed by the following set of equations:

$$\frac{dP}{dt} = T(f_P(R)P - m_P P - \sum_{i=1}^{2} g_i(P)Z_i)$$
$$\frac{dZ_i}{dt} = T(e_i g_i(P)Z_i - m_{Z_i}Z_i). \tag{3}$$

For the remainder of the season there are no resources present, so one can set $R = f_R(R) = 0$.

In the equations above, R is the amount of nutrient, P is the nutrient content of phytoplankton, and Z_i is the nutrient content of the zooplankton species i. Here, f and g_i are both type II functional responses (shown in figure 5), in which the consumption rates increase with the prey densities until reaching saturation values. The functions are given by the Michaelis-Menton equation: $f_P(R) = \frac{v_R R}{R + k_R}$ and $g_i(P) = \frac{v_i P}{P + k_i}$, where v is maximum intake of resources and k is the half saturation constant. The parameter e is dimensionless, trophic, and has a value greater than one. The mortality rates

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of phytoplankton and zooplankton i are given by m_p and m_{z_i} respectively. The period is represented by T. The system is again closed, so $R_{total} = R + P + \sum_{i=1}^{2} Z_i$.
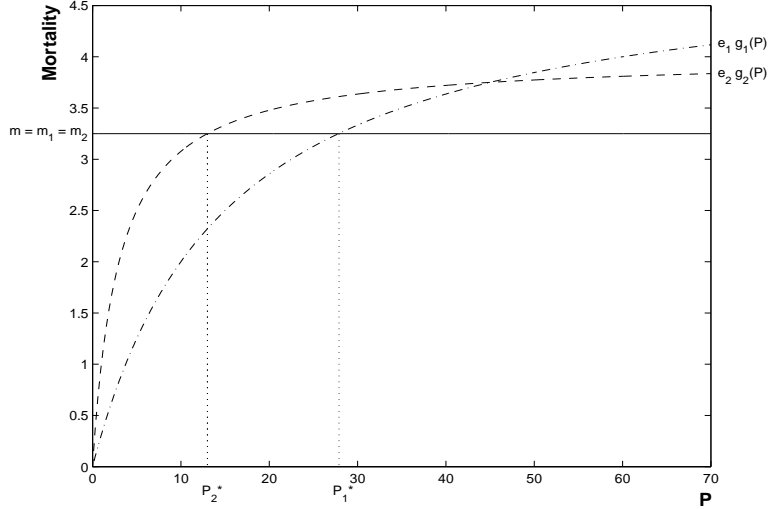

Figure 5: Type II functional responses. $P_i^\star$ represents the minimum amount of resources needed for survival of species i. It is evident that zooplankton species 2 should prevail at low phytoplankton levels in this particular situation.

If a type I functional response was implemented for the zooplankton species, then one zooplankton would always dominate the other and the system dynamics would reduce to the case of the chain discussed earlier. Because type II functional responses are used, interesting behavior can be observed for a particular combination of parameters. Zooplankton 1 has good competitive ability when photoplankton are abundant, whereas the other is a good competitor when phytoplankton are scarce. The two competing zooplankton species then can both establish exclusive dominance as the season

progresses, as illustrated in the numerical simulation in figure 6.

In the abstract case, we can specify the growth of the phytoplankton and zooplankton at a very general level. Let $\lambda_{j,k} = \frac{dj}{jdt}$ denote the eigenvalue of species j in state k. In the 0 state $\lambda_{P,0} > 0$, because P can invade a monoculture of resource and $\lambda_{Z_i,0} < 0$, because in absence of P, Z_i's are not able to grow. The P state is characterized by: $\lambda_{P,P} = 0$, because P has reached an equilibrium and $\lambda_{Z_i,P} > 0$, because P has entered the system, so Z_i has enough nutrients to grow. In the PZ_1 state: both λ_{P,PZ_1} and $\lambda_{Z_1,PZ_1} = 0$, because P and Z_1 are in equilibrium and $\lambda_{Z_2,PZ_1} > 0$, because Z_2 can invade the system. In the PZ_2 state: $\lambda_{P,PZ_2} = \lambda_{Z_2,PZ_2} = 0$, because P and Z_2 are in equilibrium, whereas Z_1 is dying, hence $\lambda_{Z_1,PZ_2} < 0$. Let $\lambda_{j,-}$ also denote the dying phase for species j lasting from pT to T during a period.

In the model presented here, we let

$$\hat{R} = R^\star = \frac{m_P k_R}{v_R - m_p}, \quad \hat{P} = R_{total} - R^\star, \text{ and } P_i^\star = \frac{m_{Z_i} k_i}{e_i v_i - m_{Z_i}}.$$

Upon subsitution we obtain,

$$\lambda_{P,0} = -m_P + f_P(R_{tot}), \quad \lambda_{Z_i,0} = -m_{Z_i}$$
$$\lambda_{P,P} = 0, \quad \lambda_{Z_i,P} = -m_{Z_i} + e_i g_i(\hat{P})$$
$$\lambda_{P,PZ_1} = \lambda_{Z_1,PZ_1} = 0, \quad \lambda_{Z_2,PZ_1} = -m_{Z_2} + e_2 g_2(P_1^\star)$$
$$\lambda_{P,PZ_2} = \lambda_{Z_2,PZ_2} = 0, \quad \lambda_{Z_1,PZ_2} = -m_{Z_1} + e_1 g_1(P_2^\star)$$
$$\lambda_{P,-} = -m_P, \quad \lambda_{Z_i,-} = -m_{Z_i}$$

The switching times between various regimes can be readily computed utilizing the equilibrium stability analysis and the linearization principles.
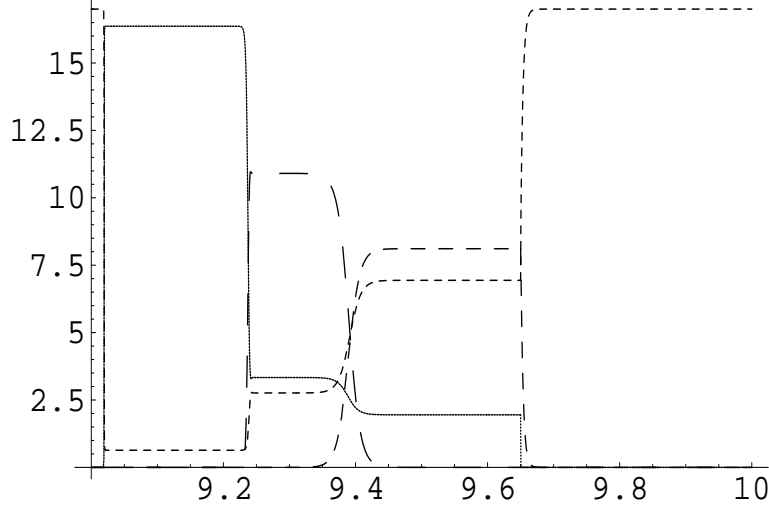
Figure 6: Numerical simulation with $T = 2900$, $R_{tot} = 17$, $p = 0.65$, $c_1 = 0.22$, $v_1 = 1$, $v_2 = 1$, $k_1 = 3.9$, $k_2 = 20$, $e_1 = 0.3$, $e_2 = 0.7$, $m_p = 0.14$, $m_{Z_1} = 0.1$, and $m_{Z_2} = 0.1$. The smallest-dashed line resprents the resource, the solid line indicates the phytoplankton, the largest-dashed line indicates the first phytoplankton, and the middle-dashed line indicates the second phytoplankton.

The time t_1, when the phytoplankton first emerges gaining a stable equilibrium is found from the fact that the per capita rate of change averaged over the whole period must vanish: $\int_0^1 \lambda_{P,k} d\tau = 0$. Expanding the integral we get: $\int_0^{t_1} \lambda_{P,0} d\tau + \int_p^1 \lambda_{P,-} d\tau = 0$. Solving for t_1 we obtain the following expression:

$$t_1 = \frac{(-1+p)\lambda_{P,-}}{\lambda_{P,0}} \ .$$

The analytical expressions for the emergence times t_2 and t_3 of respectively fast growing and good competitor zooplankton species are too complex and

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will not be presented here. For $t \in [0, t_1]$ all species are near zero; when $t \in [t_1, t_2]$, a stable population of phytoplankton emerges and prevails; when $t \in [t_2, t_3]$, a stable population of phytoplankton and the first zooplankton prevails; when $t \in [t_3, \text{p}]$ – coexistence with phytoplankton and the second zooplankton species; when $t \in [\text{p}, 1]$ – both populations rapidly decline to zero.

The two competing zooplankton species dominate at different ranges of parameter p, as illustrated by the diagram in figure 7. Depending on the value of p, the system has enough time to reach the state of P equilibrium, to take one of the branches in figure 4, or to switch between the zooplankton competitors, provided, of course, that the parameters for the zooplankton make one the fast grower and the other the good competitor.
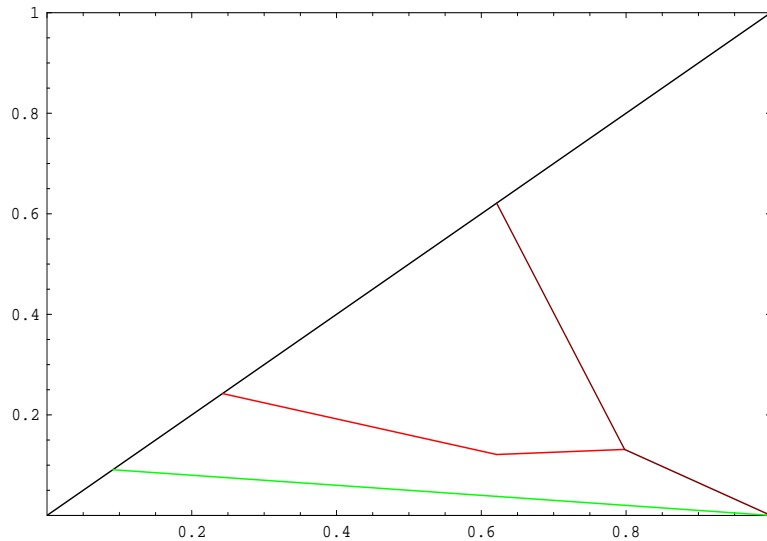

Figure 7: Bifurcation diagram of the successional dynamics within a period under seasonal forcing with long period as a function of p.

5   Conclusions

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.

For the food chain with one zooplankton, 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 the 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.

For the food web with two zooplankton their functional responses contribute significantly to the nature of the system dynamics. That is because for most cases one zooplankton dominates the other and the system is reduced to the first type discussed above. Even if there are two zooplankton species, one of which is a fast grower and the other one is the good competitor, other parameters need to be adjusted in order to witness a sizable presence of both during a period. One of the most influential parameters is the length of the season's growing period. For its intermediate values the growing season is not too long so one can see first the phytoplankton and then the fast grower emerge, but it is long enough for the good competi-

tor to appear and drive out the other zooplankton species. The system's behavior can transition from phytoplankton existing alone to coexistance of phytoplankton and one zooplankton species to a switching in dominance of zooplankton species to extinction of all species.

For the future research the described model in a similar way can be extended to more than two zooplankton species. It is believed that similar behavior will be observed and a hierchy of dominance between the various zooplankton species can be established, each species having the best competitive ability over the others for a fixed level of its resource.

Acknowledgements

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