

MATHEMATICAL MODELING OF PLANKTON PATCHINESS

by

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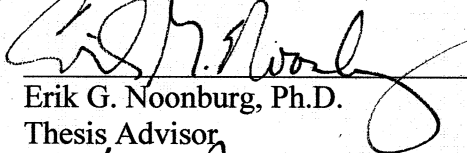
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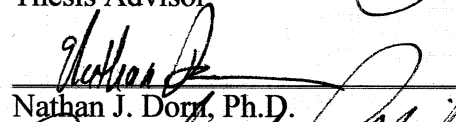
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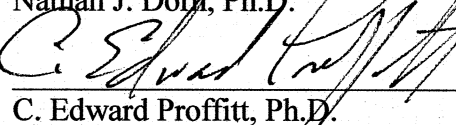
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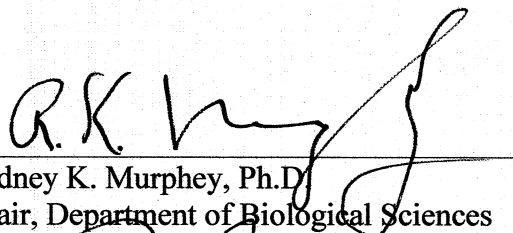
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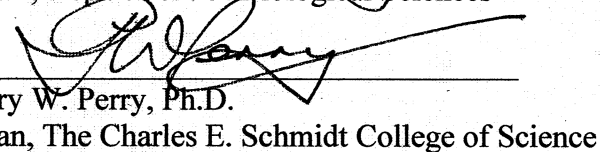
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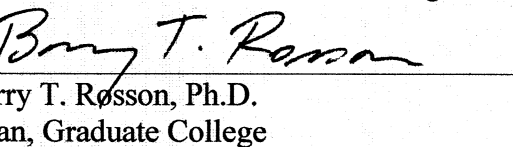
  
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## ABSTRACT

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In natural systems, it has been observed that plankton exist in patches rather than in an even distribution across a body of water. However, the mechanisms behind this patchiness are not fully understood. Several previous modeling studies have examined the effects of abiotic and biotic factors on patch structure. Yet these models ignore a key point: zooplankton often undergo diel vertical migration. I have formulated a model that incorporates vertical movement into the Rosezweig-MacArthur (R-M) predator-prey model. The R-M model is stable only at a carrying capacity below a critical value. I found that adding vertical movement stabilizes the system even at a high carrying capacity. By analyzing temporal stability and spatial structure, my results show that vertical movement interacts with carrying capacity to determine patch structure.

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## INTRODUCTION

Plankton is a classic system for the study of predator-prey interactions. Plankton constitute the base of the food web in many freshwater and marine systems, and higher trophic levels may be tightly linked to plankton productivity. The predator-prey system of zooplankton and phytoplankton exhibits both vertical and horizontal structure (Omori and Hamner, 1982, Sommer 1996). For example, in many systems, the phytoplankton stay in the upper waters (epilimnion), where they can photosynthesize. The zooplankton undergo diel vertical migration between the deeper water (hypolimnion) and the epilimnion (Stich and Lampert 1981, Gliwicz 1986, Tsuda et al. 1993, Hays et al. 1995, Haupt et al. 2009). This migration is generally thought to be a response to visual predators in the epilimnion, where zooplankton must feed (e.g., Stich and Lampert 1981, Gliwicz 1986, Huntingford and Metcalfe 1986). Zooplankton have swimming appendages which allow them to move on their own in the water. The zooplankton are so small that, to them, water appears to be extremely viscous and although the zooplankton can move on their own through the water, they cannot move very easily or very fast (Sommer 1996).

Plankton does not exist in an evenly distributed 'blanket' across any body of water. Even in open water (e.g., mid-lake or ocean), a habitat that appears to have the same conditions throughout, plankton exhibit horizontal patchiness (Okubo 1971, Folt et al. 1993, Roman



et al. 2005, Louette and De Meester 2007, Mitchell et al. 2008). A plankton patch is defined as a surface water mass that contains a concentration of organisms that is several times greater than the concentration in the background or surrounding area (Bainbridge, 1957). This horizontal structure may play a role in the temporal stability of plankton populations.

There are many methods of observing plankton patches, from the purely observational method of simply looking at them from on board a ship, to plankton tows where a mesh screen captures the plankton for quantitative analysis, to the recent method of using an optical plankton counter (OPC) which counts the plankton without capturing them. Stockwell et al. (2002) used the OPC to examine zooplankton biomass and spatial structure in Lake Erie. They looked at several different transects and found that plankton exhibited a horizontal spatial pattern across a continuum of spatial scales. This information establishes that plankton does occur in patches in a natural environment, and not only in an open water environment, but in a littoral one as well. The spatial scale of the heterogeneity observed by Stockwell et al. varies at a smaller scale than would be expected for the nutrients in the system (e.g. Abbott et al. 1982). This suggests that the patch heterogeneity is not simply driven by underlying heterogeneity in the abiotic environment.

This patch heterogeneity has an impact on the trophic levels above it. Small fish and fish larvae feed on the zooplankton and so the planktonic spatial structure will affect the foraging behavior of these fish (Sommer, 1996). It has been shown in several

experiments and models that the zooplankton patchiness does influence the swimming and feeding behaviors of some zooplankton predators (MacKenzie and Kjerboe 1995, Pitchford and Brindley, 2001).

Predator-prey interactions (and consumer-resource interactions in general) are important components in communities. Trophic structure has been examined in a multitude of studies. One such example, Hairston, Smith, and Slobodkin's 1960 paper on community structure, develops a model (the HSS model) of trophic structure based on qualitative arguments derived from observations. One of the arguments they propose is that top predators are limited by their resource, in a density-dependent manner, while their prey are rarely food-limited and are more likely to be predator-limited. In general, the HSS model suggests that each trophic level is either regulated from above or below. The qualitative HSS model can be written in quantitative form with the Lotka-Volterra predator-prey equations.

The Lotka-Volterra model (LV model) predicts a cyclical relationship between predator and prey. In a graphical representation of the LV model (time vs. population size), the peak of the predator's oscillation lags behind that of the prey. However, this cycle is characterized by a high peak followed by an extreme low, which in nature would represent an extinction (as natural populations cannot usually survive after reaching such an extreme low). This phenomenon has led to modifications of the LV model in order to increase realism and also to look for a stabilizing mechanism. The LV model can be modified to include logistic growth; this model is commonly referred to as the

Rosenzweig-MacArthur model (1963). This model has a type II functional response and is characterized by a humped prey isocline and a vertical predator isocline. The model becomes more stable as the community's equilibrium moves to the right of the hump and less stable as the equilibrium moves to the left. This leads us to the "paradox of enrichment". Rosenzweig (1971) showed that enriching a system (for example, by increasing the amount of nutrients entering) usually leads to instability of the interaction between consumer and resource. Therefore, a highly productive system is predicted to be an unstable one. However, observations from many freshwater systems suggest that this destabilization does not occur (McCauley et al. 1996). How is it that real planktonic systems are temporally stable yet they are predicted to be otherwise? Does spatial heterogeneity affect temporal stability?

One early study (Huffaker, 1958) found that one predator-prey system exhibits an oscillatory relationship. Using two species of mites as the predator and prey (*Typhlodromus occidentalis* and *Eotetranychus sexmaculatus*, respectively), Huffaker built 'universes' of increasing complexity in order to study the effects of spatial structure on the stability and persistence of a system. Each universe consisted of a number of oranges, with varying areas exposed for the food source. In a one-orange system, the populations of mites followed an oscillation and then went to extinction, consistent with the LV model. The more complex systems (more oranges with more barriers) delayed the time of the extinction. This delay implies that a system with greater spatial heterogeneity is more stable and persists longer than a simpler system. In this example, it is possible that the spatial heterogeneity contributes to the temporal stability.

What are the drivers of this spatial heterogeneity in plankton populations? What contributes to the patchiness of plankton? Stability of the system is a key factor. A natural plankton system exhibits temporal stability (e.g., Malchow 1993, Murdoch and McCauley 1985, McCauley and Murdoch 1987, 1990). A temporal stability analysis can be conducted on a model to determine if the system under consideration is temporally stable or unstable (more about this in the *Models and Methods* section below) in order to determine the validity of the model in question. An analysis of the spatial patterns is also useful in determining the legitimacy of the model. Spectral analysis is a common method of examining the spatial scale of patch structure (e.g., Steele and Henderson, 1992, Vasseur and Gaedke, 2007). These analyses help in examine two main questions:

- 1) How does vertical movement influence spatial structure?
- 2) How does vertical movement influence temporal stability?

The answers to these questions may assist in determining the relationship between stability and heterogeneity.

### **Background Theory**

There have been several theoretical explanations for the patchiness of plankton. Here I will describe three key models. All three of these models are based on a two-species system. Also, all three use the following notation:  $P$  is phytoplankton,  $Z$  is zooplankton and  $t$  is time. Here I present the equations for the temporal, population dynamics only, omitting the spatial components of the models.

The model proposed by Levin and Segel (1976) relies on diffusive instability to generate patches in predator and prey densities: diffusion (or movement, more generally) destabilizes the dynamics of phytoplankton and zooplankton to produce patterns in a system that might otherwise be spatially homogeneous. Imagine a system where zooplankton and phytoplankton are distributed evenly over a section of water. A local stochastic perturbation occurs, causing a peak in the distribution of, e.g., phytoplankton density, which causes zooplankton density to increase. Zooplankton move faster (according to this model) and that results in a wider distribution peak than that of the slower moving phytoplankton. In the areas surrounding the peak, the zooplankton are more dense relative to the equilibrium that can be supported by the phytoplankton. This keeps the densities of the phytoplankton lower around the peak and high only at the peak, where they “escape” the slower-growing zooplankton. Given sufficiently strong nonlinearity in the predator-prey interaction, an initial perturbation will cause a dynamic spatial pattern of patch growth and decay (just as the Rosenzweig-MacArthur model can generate oscillatory dynamics in time).

Levin and Segel formulated their model as:

$$(1) \quad \frac{dP}{dt} = aP + eP^2 - bPZ$$

$$(2) \quad \frac{dZ}{dt} = cPZ - dZ^2$$

In equations (1) and (2),  $a$ ,  $b$ ,  $c$ ,  $d$ , and  $e$  are all assumed to be positive numbers (these parameters are not easily interpreted in biological terms). These equations, as presented, are for the temporal dynamics. The Levin and Segel model has a Type I functional

response but contains somewhat unusual nonlinear terms in the predator and prey equations. Still, this nonlinearity in the predator-prey interaction is necessary to obtain the diffusive instability that is the end result of this model. However, the main problem with the Levin and Segel theory is that it predicts the wrong patch scale for zooplankton relative to phytoplankton; their model predicts zooplankton will vary at a larger spatial scale than phytoplankton, whereas the opposite pattern is observed in real systems (e.g., Mackas et al. 1985). Applying the Levin and Segel model using phytoplankton as the faster moving group does not give the same results. In this system, the zooplankton peak would be the narrower, higher, one and this would push the phytoplankton density further down at the peak. In the surrounding areas, the zooplankton density is lower relative to the equilibrium and so the phytoplankton will increase. The end result is a spatially homogeneous system.

Another theory, proposed by Steele and Henderson (1992), focuses on continual perturbation as the method of generating plankton patches. They used the following model:

$$(3) \quad \frac{dP}{dt} = aP \left( 1 - \frac{P}{k} \right) - \frac{bZP^2}{(1+P^2)}$$

$$(4) \quad \frac{dZ}{dt} = \frac{b'ZP^2}{(1+P^2)} - dZ^2$$

In equations (3) and (4),  $a$  is the rate of prey increase,  $b = b' = 1$  and  $d$  is the death rate of the predator. Again, the model presented here represents temporal dynamics only. It contains a Type III functional response with logistic growth in the prey. Steele and

Henderson hypothesized that zooplankton are continually perturbed by fish predation and other stochastic events at the level of individual zooplankton and this, in turn, perturbs the phytoplankton. This model can predict the empirically-seen patch scale; the fish predation perturbs the zooplankton at a small (local) scale whereas the phytoplankton are following that perturbation, which results in a larger spatial scale. A problem with this model, however, is that the spatial scale of perturbation in the zooplankton was arbitrarily chosen and was not based on a biological mechanism.

A third alternative, proposed by Abraham (1998) suggests that differences in the life histories of zooplankton and phytoplankton play a large role in forming the spatial patterns of a plankton population. Zooplankton have a slower response to changing resource density because of their longer maturation time whereas phytoplankton have a fast reproductive rate. Phytoplankton density is directly related to the amount of nutrients available to them and this leads to variation at the (large) spatial scale of variation in nutrient concentration. Abraham modeled the difference in time scales by adding a delay to zooplankton reproduction:

$$(5) \quad \frac{dC}{dt'} = \alpha(C_0 - C)$$

$$(6) \quad \frac{dP}{dt'} = P \left( \frac{1-P}{C} \right) - PZ$$

$$(7) \quad \frac{dZ}{dt'} = P(t'-\tau)Z(t'-\tau) - \delta Z^2$$

This model is markedly different from the models presented above in that it includes an equation for the change in carrying capacity,  $C$  (Equation (5)), which is driven by an

underlying spatial gradient in nutrient concentration. In equations (5), (6), and (7),  $\alpha$  is the relaxation rate of the carrying capacity,  $t' = rt$  ( $t'$  is the dimensionless time) where  $r$  is the phytoplankton growth rate,  $\tau/r$  is the time taken for the zooplankton to mature, and  $\delta$  is the zooplankton death rate. The Abraham model is presented here as a single-compartment model. Abraham's model looks at sections of water, which he terms "parcels". A body of water is simulated as parcels, whose movement through a nutrient gradient is driven by turbulent stirring. In a given parcel of water, as the nutrient concentration increases, the phytoplankton density increases along with it, leading to an eventual increase in zooplankton density. However, zooplankton patches are broken up by turbulence rapidly relative to the rate at which they form by reproduction.

This model is arguably the most successful explanation for the observed difference in spatial scale of phytoplankton and zooplankton patches. Yet it ignores the vertical movement of zooplankton (e.g., vertical migration, mixing), which potentially leads to differences in the horizontal movement rates of phytoplankton compared to zooplankton. For example, in the epilimnion, the wind-driven turbulence might be greater than in the hypolimnion. Thus, organisms in the epilimnion would have a faster horizontal movement rate than do organisms in the hypolimnion. Additionally, zooplankton move faster than phytoplankton (in the epilimnion) via active swimming, but only zooplankton migrate to the hypolimnion (where they stay for some part of the day). Because of their time spent in the hypolimnion, the zooplankton movement might (on average) be slower than that of phytoplankton.



As discussed above, the Levin and Segel model would be more accurate if it predicted the correct patch scale (the scale of heterogeneity seen in a natural system). Steele and Henderson's model relies on an arbitrary perturbation scale. Although the model predicts the correct scale of zooplankton relative to phytoplankton, it does so without reference to a natural mechanism. Abraham's model does not include the zooplankton's ability to move on its own; it includes only the turbulence of the water as the factor driving the predator's movement. It is possible that the turbulence alone is not what is causing the heterogeneous patch structures, although Abraham accounts for the differences in the spatial scales (between the two plankton types) by including a time lag in the zooplankton birth rates as compared to those of the phytoplankton. All three of the above models have a nonlinear death rate. This nonlinearity adds a potentially confounding factor (e.g., greater temporal instability) when trying to determine the effects of spatial dynamics on plankton patchiness.

The zooplankton (in many natural systems) travel vertically between the epilimnion and the hypolimnion as well as horizontally across a transect of water. The phytoplankton exhibit primarily horizontal movement driven by turbulence. This purely horizontal movement creates a diffusive-like appearance to the phytoplankton population (much like the Levin and Segel model). However, the vertical movement of the zooplankton potentially slows this diffusive behavior and causes a more choppy patch structure, in other words, a smaller patch scale. Adding vertical migration also makes for a more realistic model (e.g., Stich and Lampert 1981, Gliwicz 1986, Tsuda et al. 1993, Hays et al. 1995, Haupt et al. 2009). By including a vertical component in my model, I am

examining the effects of this reduction in zooplankton horizontal movement rate on the scale of heterogeneity in the zooplankton and phytoplankton. I want to omit as many confounding factors as I can and focus purely on vertical migration as a possible cause of naturally observed patch scales. In addition, I am including a parameter for the actual, non-turbulence-driven, movement of the zooplankton. I want my model to match, as closely as possible, the natural environment while still focusing on one aspect of patch formation: the vertical movement of zooplankton. In the following section, I will describe my model and explain the historical context and the foundation for my model. Unlike the above three models, my model is derived from the Rosenzweig-MacArthur model, with vertical movement added as a factor.

## MODELS AND METHODS

The Rosenzweig-MacArthur (R-M) predator-prey model (Rosenzweig and MacArthur, 1963) is the basic foundation for my model. The following is the set of R-M equations, one for the prey (phytoplankton,  $P$ ) and one for the predator (zooplankton,  $Z$ ).

$$(8) \quad \frac{dP}{dt} = rP \left( 1 - \frac{P}{K} \right) - \frac{aPZ}{1 + aT_h P}$$

$$(9) \quad \frac{dZ}{dt} = \frac{\alpha e P Z}{1 + \alpha T_h P} - dZ$$

In the above,  $r$  is the rate of reproduction of the phytoplankton,  $K$  is the carrying capacity,  $\alpha$  is the attack rate,  $T_h$  is the handling time and  $e$  is the conversion efficiency. The carrying capacity is assumed to be proportional to the amount of nutrients in a given body of water, i.e., eutrophic (nutrient-rich) systems have high  $K$  and oligotrophic (nutrient-poor) systems have low  $K$ .

Murdoch et al. (1998) examined the inconsistencies between theoretical models (e.g., the paradox of enrichment) and real, observed, data. The Murdoch paper compares the R-M model to observed plankton behavior as opposed to earlier papers which compared plankton behavior to the Lotka-Volterra model (e.g., Oksanen et al., 1981, McCauley et al., 1988, Leibold 1989, Sarnelle, 1992). Murdoch adjusted the R-M model to better reflect the way in which plankton actually feed (plankton are filter feeders). There is no

attack rate ( $\alpha$ ) and no handling time ( $T_h$ ); instead there is  $E_h$ , the half-saturation density of edible algae and  $I_{max}$ , the maximum intake rate.

The model (hereafter referred to as the Non-Spatial Model) used by Murdoch et al. (1998) is:

$$(10) \quad \frac{dP_i}{dt} = rP_i \left( 1 - \frac{P_i}{K} \right) - \frac{I_{max} P_i Z_{S,i}}{E_h + P_i}$$

$$(11) \quad \frac{dZ_{S,i}}{dt} = \frac{eI_{max} P_i Z_{S,i}}{E_h + P_i} - d_S Z_{S,i}$$

Murdoch et al. derive a local stability requirement, given by:

$$(12) \quad K < E_h \frac{(eI_{max} + d_S)}{(eI_{max} - d_S)}$$

This indicates that the carrying capacity,  $K$ , must be below the right side of Equation (12) in order for the system to be temporally stable.

The R-M model ignores the vertical and horizontal spatial structure (McCauley et al., 1996). The R-M model is representative of what would happen in a single compartment of my model, with no horizontal or vertical movement.

### **Spatially Structured Model**

My model is based on Equations (10) and (11), with the inclusion of vertical, as well as horizontal, structure. The above deal with local stability in only the temporal sense, while I am examining stability both temporally and spatially.

A body of water is split into  $N$  horizontal compartments, each with a shallow region and a deep region. The vertical component is represented by the movement of the zooplankton between shallow and deep; this adds an equation to the standard R-M model.

My model is mathematically expressed by the following equations ( $P$  is phytoplankton,  $Z_S$  is zooplankton in the shallow region,  $Z_D$  is zooplankton in the deep region, and  $i$  is the compartment number):

$$(13) \quad \frac{dP_i}{dt} = rP_i \left(1 - \frac{P_i}{K}\right) - \frac{I_{\max} P_i Z_{S,i}}{E_h + P_i} - m_P (P_i - P_{i-1}) - m_P (P_i - P_{i+1})$$

$$(14) \quad \begin{aligned} \frac{dZ_{S,i}}{dt} = & \frac{eI_{\max} P_i Z_{S,i}}{E_h + P_i} - d_S Z_{S,i} - m_{SZ} (Z_{S,i} - Z_{S,i-1}) - m_{SZ} (Z_{S,i} - Z_{S,i+1}) \\ & - m_V (Z_{S,i} - Z_{D,i}) \end{aligned}$$

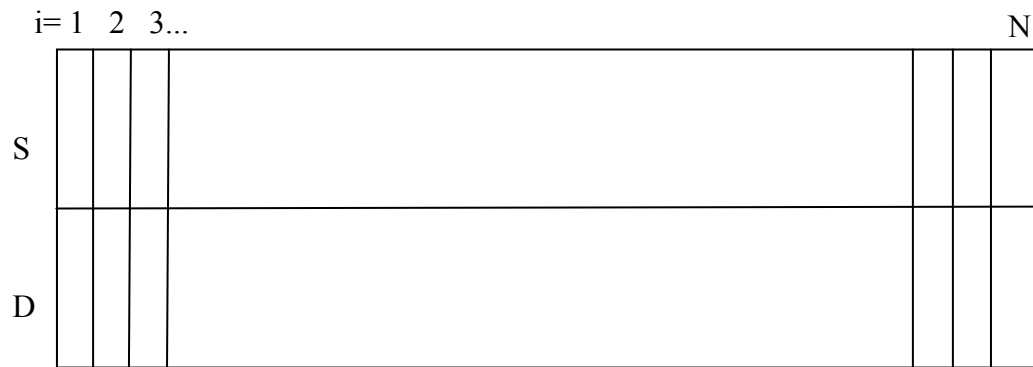
$$(15) \quad \begin{aligned} \frac{dZ_{D,i}}{dt} = & -m_V (Z_{D,i} - Z_{S,i}) - m_{DZ} (Z_{D,i} - Z_{D,i-1}) \\ & - m_{DZ} (Z_{D,i} - Z_{D,i+1}) - d_{D,i} Z_{D,i} \end{aligned}$$

PARAMETER	DEFINITION	UNITS	VALUES
$r$	Rate of increase of phytoplankton	day <sup>-1</sup>	0.5
$K$	Carrying capacity	(mg C) L <sup>-1</sup>	varies
$I_{max}$	Maximum intake rate	day <sup>-1</sup>	1
$E_h$	Half-saturation density of edible algae	(mg C) L <sup>-1</sup>	0.16
$e$	Assimilation efficiency	unitless	0.5
$d_S$	Death rate of zooplankton in the shallow region	day <sup>-1</sup>	0.12
$d_D$	Death rate of zooplankton in the deep region	day <sup>-1</sup>	0.12
$m_P$	Horizontal movement of phytoplankton	day <sup>-1</sup>	0.05
$m_{SZ}$	Horizontal movement of zooplankton in the shallow region	day <sup>-1</sup>	0.5
$m_V$	Vertical movement of zooplankton	day <sup>-1</sup>	varies
$m_{DZ}$	Horizontal movement of zooplankton in the deep region	day <sup>-1</sup>	0

**Table 1: Definition of the parameters. Units taken from Murdoch et al., 1998. Values for  $I_{max}$ ,  $E_h$ ,  $e$ ,  $r$ , and  $d_S$  also taken from Murdoch et al., 1998.**

The spatial components of my model are represented by the following parameters:  $m_P$  is the horizontal movement of the phytoplankton,  $m_{SZ}$  is the horizontal movement of the zooplankton in the shallow compartment,  $m_V$  is the vertical movement of the zooplankton, and  $m_{DZ}$  is the horizontal movement of the zooplankton in the deep compartment.

The compartment structure is graphically represented in Figure 1, in which  $S$  stands for shallow and  $D$  stands for deep. For  $i=1$ , there is no movement to the left. In other words, there is no movement in the  $i-1$  direction. For  $i=N$ , there is no movement to the right, i.e., there is no movement in the  $i+1$  direction. The plankton in any middle compartment can move both to the right and to the left of their original compartment. For example, for  $i=29$ , the plankton in that compartment can either move right to compartment number 30 or left to compartment number 28.



**Figure 1: Schematic of the spatially structured model.**

I used a 1000-compartment model ( $N=1000$ ) to examine the dynamics of the plankton population. In my model, the lengths of the compartments are arbitrary, as the spatial scale is relative to the movement of plankton. Analyzing the stability of the model, both spatially and temporally, is my next step as I attempt to find answers as to why plankton exist in patches.

### **Temporal Stability**

Stability analysis is a mathematical and purely theoretical way of looking at the stability of the system at equilibrium. If a system at equilibrium undergoes a perturbation and

then, after some period of time, returns to its equilibrium, that equilibrium is considered stable. If the system never recovers its equilibrium state after a perturbation, it is considered unstable. Many systems have both a stable and an unstable domain; that is, there are factors that push a stable system into instability and vice versa. These factors include the starting conditions (whether the system starts near equilibrium) and the nature of the perturbation (there will be some perturbations from which the system cannot recover equilibrium). The stable domain of the system depends on the values of the parameters of that system (in this case, the parameters of a natural plankton system as given in Murdoch et al. 1998). The stability boundary is the boundary between the stable and unstable domains (Gurney and Nisbet, 1998). A key point in stability analysis is finding this boundary and discovering what pushes the system from stability to instability and back again.

Local stability of an equilibrium can be assessed by finding the eigenvalues of the system of equations linearized about the equilibrium. An equilibrium is stable if the real parts of all eigenvalues are negative, which can be determined via the Routh-Hurwitz conditions for the model (see, e.g., Edelstein-Keshet 1987, pp. 231-236). The standard method is outlined in Appendix A.

The equations of the system are the differential equations of my model (Equations (13), (14), and (15)) with a few differences. The stability analysis is concerned with temporal stability so I am analyzing a single-compartment version of my model (including both shallow and deep regions). In a single-compartment system, the horizontal movement



parameters,  $m_P$ ,  $m_{SZ}$ , and  $m_{DZ}$  are all equal to zero (i.e., there is no horizontal movement). The positive equilibrium for this system (see Equations (20), (21), and (22) in Appendix A) is used in the characteristic equation that results from the Jacobian matrix (Equation (32) in Appendix A).

The Jacobian matrix is composed of the coefficients of the linearized system of differential equations. Local stability of the equilibrium can be determined from the eigenvalues of the Jacobian. If all eigenvalues have negative real parts, the system will return to equilibrium from a small perturbation. A positive eigenvalue indicates that perturbation will grow.

Eigenvalues are often difficult (and at times impossible) to calculate analytically. If this is the case, the Routh-Hurwitz conditions serve as an indicator of stability. When the coefficients of the characteristic equation fit the Routh-Hurwitz conditions, it leads to the conclusion that the eigenvalues have negative real parts and that the system is indeed stable.

The Routh-Hurwitz stability conditions are the standard criteria for ascertaining the stability of a system. Given the characteristic equation, a set of calculations are done using only the coefficients of that equation in order to find the roots. The results of these calculations (the roots of the equation) must fit the Routh-Hurwitz conditions in order for the system to be analytically deemed as stable. These conditions are the end result of the

stability analysis. I have completed all the necessary calculations and the results are presented in the following *Results* section (see Appendix A for all calculations).

### **Spatial Scale of Patch Structure**

In conjunction with the stability analysis outlined above, I am also conducting a spectral analysis. This is a means of quantifying the spatial scale of patchiness. The population dynamics equations of my model, when solved, create a time-domain graph for each compartment, i.e., the function is plotted over time. At any point in time the model predicts a pattern of population densities in the spatial domain. Spectral analysis is a way to examine the predictions with respect to frequency rather than time or space. Here, I use spectral analysis to examine the spatial heterogeneity in the structure of plankton density. A space-domain graph is converted to a frequency-domain graph using the Fast Fourier transform. This results in a spectral graph, with the function being analyzed over a set of frequencies (with frequency defined as the number of cycles per unit distance), resulting in a readable “signal” (Press et al., 1992). The spectrum allows an examination of the variance at different spatial scales.

The variance of the spectrum goes down as the number of replicate runs of the model increases (Press et al., 1992).

$$(16) \quad Var(v) = \frac{1}{N-1} \sum_{j=1}^N (v_j - \bar{v})^2$$

Equation (16) is the expression for variance, where  $N$  is the number of replicates and  $v$  is the y-axis value of any point on the spectrum. As my data is computer generated, it is

possible to have an extremely large number of replicates, thereby reducing the statistical error in the spectral plot to a negligible degree.

Along with the spectral plots, I have included autocorrelation plots as well.

Autocorrelation is related to the spectra in that they are both plots of a signal. Whereas the spectra are graphical representations of a signal, the autocorrelations are graphs of the relation of that signal to itself. The autocorrelation is a useful tool in determining whether my model plankton system exhibits a patchy structure similar to that of a real plankton system.

A way to summarize the spectral plots is to run a regression (using a linear model) on the output and then plot the resulting slopes. Figure 2 is a sample plot. Its purpose is to assist in easy identification of the various regions of the plot and to explain what is occurring in a general sense. In these types of charts, the line that is uppermost has the shallower slope and, therefore, is the population with the smaller patch scale. This shallower slope has a larger value because all the values are negative; the value closest to zero is the larger one.

Looking at Figure 2, to the left of the dashed line, the phytoplankton population is the uppermost line and thus, this is the population with the smaller patch scale. To the right of the dashed line, the population lines “switch” and now the zooplankton population is the uppermost line and the one with the smaller patch scale. This situation, where the

zooplankton exhibit the smaller patch scale, is the pattern that is observed in nature (e.g., Mackas et al. 1985, Folt et al. 1993, and Mitchell et al. 2008).

## RESULTS

I varied the carrying capacity,  $K$ , and ran the model (Equations (13), (14), and (15)) to look at the way in which vertical movement had an effect for values of  $K$  at either side of the stability boundary. In the single compartment model (Equation (12), with the parameters in Table 1),  $K$  must be less than 0.26 in order for the system to be stable without any vertical movement. Using this as my “baseline” stability boundary, I used  $K=0.22$  as the low value and  $K=0.28$  as the high value. These particular high and low values of  $K$  are used as endpoints throughout the rest of this paper.

These results graphically present various aspects of the spatially structured model. First I examine temporal stability. Then, various scenarios are presented: varying vertical movement at low  $K$  and high  $K$ , and varying  $K$  at zero  $m_V$ , low  $m_V$ , and high  $m_V$ .

### **Temporal Stability Analysis**

I followed the steps of the stability analysis (see Appendix A). The Routh-Hurwitz conditions proved to be intractable. I was unable to find an analytic solution for the stability boundary as a function of  $K$  or  $m_V$ . I used a software package (R, v. 2.5.1) to numerically calculate the real part of the largest eigenvalue as  $m_V$  increased (Figure 3 and Figure 4). If the largest eigenvalue is negative, then all of the eigenvalues are negative and the equilibrium is stable.

Figure 3 displays the largest eigenvalue vs.  $m_V$  at low  $K$  ( $K=0.22$ ). At this low value of  $K$ , the eigenvalue is always negative, indicating a temporally stable system. This is in agreement with the stability boundary discussed above where  $K$  must be less than 0.26 (Equation (12)) for the plankton system to be stable. At  $m_V=0$ , the model is the same as the Rosenzweig-MacArthur model. But, as  $m_V$  goes up, the system remains stable. This is a new result and it has possibilities for further exploration.

Figure 4 shows the largest eigenvalue vs.  $m_V$  at high  $K$  ( $K=0.28$ ). This value is above the calculated stability boundary and is in the unstable domain. At first, the eigenvalue is positive, indicating an unstable system. As the vertical movement increases, the eigenvalue decreases and becomes negative. This indicates that, although the carrying capacity,  $K$ , is in the unstable domain for the R-M model, the addition of vertical movement stabilizes the system. This is a surprising result; the R-M model predicts instability at a high  $K$ , yet this system is stable at a high  $K$  for a vertical movement rate greater than a critical speed.

### **Spectral Analysis**

I plotted the population density across space, the autocorrelation, and the spectral graph for both the phytoplankton and zooplankton populations. Figure 5 is the set of graphs at low  $K$  and Figure 6 is the set of graphs at high  $K$ . Across space, both populations of plankton exhibit variations across the compartments, i.e., they exhibit the heterogeneous structure that is characteristic of natural plankton populations. The autocorrelation graphs show that as the compartments being compared increase in distance the

correlation between population densities drops off. In other words, densities of plankton that are further away from any given point are not similar to that point. There is statistically significant autocorrelation up to some distance. This distance is the length scale of the patches. The spectral density, or variance, decreases with increasing frequency (the negative slope seen in Figure 5 and Figure 6). This means that the majority of the variance is at low frequencies. However, there are small scale patches at high frequencies, consistent with significant autocorrelation at small distances. This is qualitatively consistent with empirical data (Okubo 1971, Folt et al. 1993, Roman et al. 2005, Louette and De Meester 2007, Mitchell et al. 2008). The spectral graphs are more difficult to analyze in their present form (as in Figures 5 and 6) and the results of the regression plots are presented as slopes of regressions of the spectra.

I examined the effect of varying the vertical movement,  $m_V$ , at values of  $K$  on either side of the stability boundary in the non-spatial system. I plotted the slopes of the spectra for both phytoplankton and zooplankton on one graph to more easily compare the two.

At low  $K$ , the zooplankton always have a smaller patch scale than the phytoplankton (Figure 7). However, the difference in patch scale between the two populations decreases as the vertical movement is increased. This implies that at a very fast vertical movement rate, the patch scales converge and become equal.

At high  $K$ , the patch pattern also depends on the rate of vertical movement (Figure 8). At very low values of  $m_V$ , the phytoplankton has the smaller patch scale. As  $m_V$  goes up, the system switches and zooplankton has the smaller patch scale, again with the difference decreasing as  $m_V$  increases, implying a convergence of patch scales between the two populations.

I also examined the effects of varying the carrying capacity at different vertical movement rates. I found that, regardless of the value of  $m_V$ , zooplankton always have a smaller patch scale at low values of  $K$  and then switch to having the larger patch scale at high values of  $K$ . The basic shape of the zooplankton population line is very similar across all three graphs. At  $m_V=0$ , the zooplankton patch scale changes from smaller to larger at approximately  $K=0.25$  (Figure 9). The addition of vertical movement pushes the stability boundary slightly to the right, increasing it by a small amount. At both slow vertical movement ( $m_V=0.001$ , Figure 10), and fast vertical movement ( $m_V=0.01$ , Figure 11), the zooplankton patch scale switches at approximately  $K=0.26$ .



## DISCUSSION

### **Relating Temporal Analysis to Spectral Analysis**

In the regression plots of simulations with fixed  $m_V$  and varying  $K$  (Figures 9, 10, and 11), the patch scale switches. Zooplankton starts as the population with smaller scale patch structure and changes to the population with larger scale patch structure as the system crosses the stability boundary. This suggests that the spatial scale of patch structure may be related to the temporal stability of the underlying predator-prey interaction.

Looking at the temporal analysis in Figure 4, at a value of  $K$  above the stability boundary, the eigenvalue decreases as  $m_V$  increases. The eigenvalue becomes negative which indicates a stable system. Stability here depends on the speed of vertical movement (faster  $m_V$  leads to stability). This leads to the possibility that vertical movement is a stabilizing factor in systems with a carrying capacity beyond the stability boundary.

Increasing vertical movement has an effect similar to that of increasing the zooplankton death rate. But if vertical movement is indeed a stabilizing factor in a eutrophic system, then this presents a possible explanation for why real planktonic systems are temporally stable in spite of predictions to the contrary. This is a possible mechanism for resolving

the paradox of enrichment. The spatial heterogeneity produced by the vertical movement does seem to have an influence on temporal stability.

### **Weaknesses in the Spatially Structured Model**

My model does not represent vertical migration per se; it models vertical movement.

This movement is a first approximation of vertical migration, but it does not take several natural factors into account. One such factor is fish predation. One reason for the vertical migration of zooplankton is to avoid fish predation (e.g., Stich and Lampert 1981, Gliwicz 1986, Huntingford and Metcalfe 1986). The presence of fish in the system would possibly alter the zooplankton movement patterns; this may result in changes to the patch structure.

Also, it has been observed that zooplankton undergo diel vertical migration (Stich and Lampert 1981, Gliwicz 1986, Tsuda et al. 1993, Hays et al. 1995, Haupt et al. 2009). The spatially structured model does not include any synchronous movement, or fixed time spent, by the zooplankton in the hypolimnion. In my model, the zooplankton are moving from epilimnion to hypolimnion and directly back again.

### **For Further Study**

The spatially structured model presents some predictions that can be empirically tested.

This model predicts that vertical movement can stabilize a eutrophic system. In nature, different lakes have different nutrient levels, ranging from oligotrophic to eutrophic.

Pollution is a large factor in the eutrophication of lakes and this is a major concern for

many industries. The possibility of a viable ecosystem (from plankton up to higher trophic levels) in spite of polluted water is an intriguing one. Based on the model's predictions, the varying nutrient levels should create variations in patch structure among different lakes; the effect of the differing patch structures on higher trophic levels can be examined as well, theoretically and experimentally.

Another idea that can be explored experimentally is the parameterization of the movement rate. The movement rate will determine the length scale of the compartments. This length scale can be quantitatively tested against real data, for example, data gathered from an OPC (e.g., Stockwell et al. 2002). It would be possible to compare the power spectra from the theoretical model with that of the empirical data and further conclusions about the model and plankton systems in general can be drawn.

An additional factor that can be investigated quantitatively is the relationship between  $K$  and  $m_V$ . There seems to be an interaction between the two that could bear further investigation.

To conclude, plankton patchiness is a complex system of various interactions. Some of these interactions, namely carrying capacity and vertical movement, are potential mechanisms for resolving theory (such as the paradox of enrichment) with observed data (plankton does exist in patches). These mechanisms may be difficult to find, but through a combination of mathematical modeling and empirical research, we may someday know why plankton exists in patches.

## APPENDIX A: STABILITY ANALYSIS CALCULATIONS

There are four basic steps necessary in order to carry out a stability analysis:

1. Define the equations to be used in the matrix.
2. Set these equations to zero to calculate the equilibrium.
3. Calculate the terms of the Jacobian matrix ( $J_{1,1}$ ,  $J_{1,2}$ , etc.).
4. Check the three conditions of the Routh-Hurwitz criteria .

### Step 1: Defining the equations.

The stability analysis examines local stability, i.e., stability in only one compartment.

Therefore, there are no compartment number labels on the variables here (in my model, compartment number is symbolized by the subscript,  $i$ ) and no horizontal movement variables ( $m_P$ ,  $m_{SZ}$ , and  $m_{DZ}$ ).

$$(17) \quad \frac{dP}{dt} = rP \left( 1 - \frac{P}{K} \right) - \frac{I_{\max} P Z_S}{E_h + P}$$

$$(18) \quad \frac{dZ_S}{dt} = \frac{e I_{\max} P Z_S}{E_h + P} - d_S Z_S - m_V (Z_S - Z_D)$$

$$(19) \quad \frac{dZ_D}{dt} = -m_V (Z_D - Z_S) - d_D Z_D$$

**Step 2: Setting equations (17), (18), and (19) to equilibrium.**

$$(20) \quad P^* = d_S + m_V \left( \frac{1 - m_V}{d_D + m_V} \right) \left( \frac{E_h}{eI_{\max} - d_S + m_V \left( \frac{1 - m_V}{d_D + m_V} \right)} \right)$$

$$(21) \quad Z_S^* = r \left( \frac{1 - P^*}{K} \right) \left( \frac{P^* + E_h}{I_{\max}} \right)$$

$$(22) \quad Z_D^* = \frac{m_V Z_S^*}{d_D + m_V}$$

**Step 3: Calculating the terms of the Jacobian matrix.**

Each component of the Jacobian matrix is a partial derivative of one of the differential equations taken with respect to one of the variables. For example,  $J_{1,1}$  is the derivative of the  $P$  equation taken with respect to  $P$  and  $J_{2,3}$  is the derivative of the  $Z_S$  equation taken with respect to  $Z_D$ . The values of the variables ( $P$ ,  $Z_S$ , and  $Z_D$ ) in the resulting equations are the values at equilibrium ( $P^*$ ,  $Z_S^*$ , and  $Z_D^*$ ).

$$(23) \quad J_{1,1} = \frac{\delta P}{\delta P} = \frac{r - 2rP^*}{K} - \frac{I_{\max} Z_S^* E_h}{(E_h + P^*)^2}$$

$$(24) \quad J_{1,2} = \frac{\delta P}{\delta Z_S} = -\frac{I_{\max} P^*}{E_h + P^*}$$

$$(25) \quad J_{1,3} = \frac{\delta P}{\delta Z_D} = 0$$

$$(26) \quad J_{2,1} = \frac{\delta Z_S}{\delta P} = \frac{eI_{\max} Z_S^* E_h}{(E_h + P^*)^2}$$

$$(27) \quad J_{2,2} = \frac{\delta Z_S}{\delta Z_S} = \frac{eI_{\max} P^*}{E_h + P^*} - d_S - m_V$$

$$(28) \quad J_{2,3} = \frac{\delta Z_S}{\delta Z_D} = m_V$$

$$(29) \quad J_{3,1} = \frac{\delta Z_D}{\delta P} = 0$$

$$(30) \quad J_{3,2} = \frac{\delta Z_D}{\delta Z_S} = m_V$$

$$(31) \quad J_{3,3} = \frac{\delta Z_D}{\delta Z_D} = -d_D - m_V$$

These terms are used to form the characteristic equation.

#### **Step 4: Checking the Routh-Hurwitz conditions.**

The characteristic equation is found by calculating the determinant of the Jacobian matrix ( $\det(J)$ ) and setting it to zero. The equation takes the following form:

$$(32) \quad \det(J) = \lambda^3 - \lambda^2 a_1 + \lambda a_2 - a_3$$

The coefficients,  $a_1$ ,  $a_2$ , and  $a_3$ , are the components of the Routh-Hurwitz conditions.

The three coefficients are calculated in Equations (36), (37), and (38), with the three variables,  $P$ ,  $Z_S$ , and  $Z_D$ , at their equilibrium values,  $P^*$ ,  $Z_S^*$ , and  $Z_D^*$ , respectively (see Equations (20), (21), and (22) above).

The Routh-Hurwitz conditions are:

1.  $a_1 > 0$
2.  $a_3 > 0$
3.  $a_1 a_2 - a_3 > 0$ .

Each component of the conditions is calculated below.

$$(33) \quad a_1 = -(J_{1,1} + J_{2,2} + J_{3,3})$$

$$(34) \quad a_2 = -(-J_{1,1}J_{3,3} - J_{2,2}J_{3,3} - J_{1,1}J_{2,2} + J_{2,3}J_{3,2} + J_{1,2}J_{2,1} + J_{1,3}J_{3,1})$$

$$(35) \quad a_3 = -\left( \begin{array}{l} J_{1,1}J_{2,2}J_{3,3} - J_{1,1}J_{2,3}J_{3,2} - J_{1,2}J_{2,1}J_{3,3} + J_{1,2}J_{2,3}J_{3,1} \\ + J_{1,3}J_{2,1}J_{3,2} - J_{1,3}J_{2,2}J_{3,1} \end{array} \right)$$

The solutions for  $a_1$ ,  $a_2$ , and  $a_3$  after substituting in the values of each  $J$  term (and cancelling out terms where appropriate) are below.

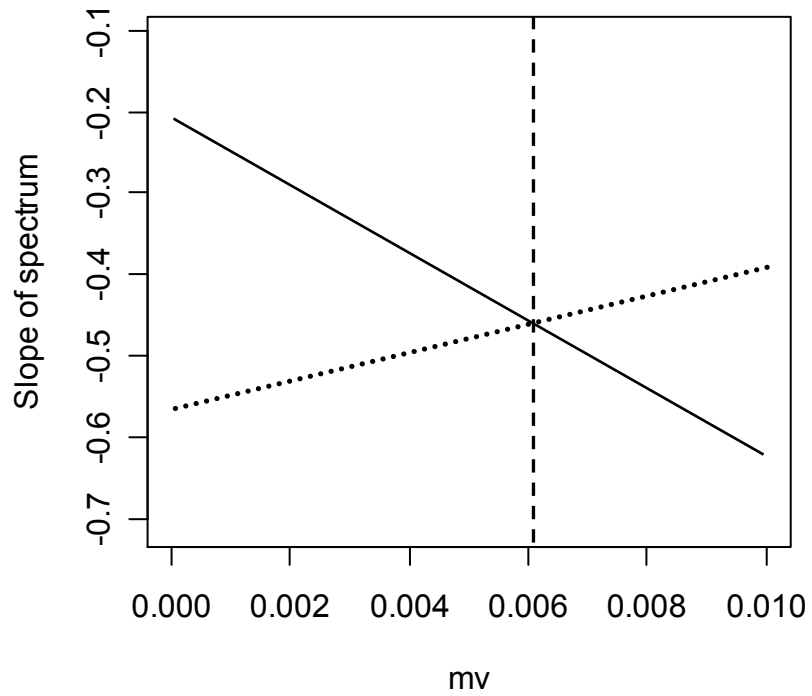
$$(36) \quad a_1 = -\left( \frac{r - 2rP^*}{K} - \frac{I_{\max} Z_S^* E_h}{(E_h + P)^2} + \frac{eI_{\max} P^*}{E_h + P^*} - d_S d_D 2 - 2m_V \right)$$

$$(37) \quad a_2 = -\left( \begin{array}{l} \left( (d_D + m_V) \frac{r - 2rP^*}{K} + \frac{I_{\max} Z_S^* E_h}{(E_h + P^*)^2} \right) + \left( (d_D + m_V) \frac{eI_{\max} P^*}{E_h + P^*} - d_S - m_V \right) \\ \left( \frac{eI_{\max} P^* r - eI_{\max} 2rP^{*2}}{E_h K + P^* K} - \frac{I_{\max} Z_S^* E_h}{(E_h + P^*)^2} \right) \\ - \left( d_S - m_V \right) \frac{r - 2rP^*}{K} \\ + \left( d_S - m_V \right) \frac{I_{\max} Z_S^* E_h}{(E_h + P^*)^2} \end{array} \right) + m_V^2$$

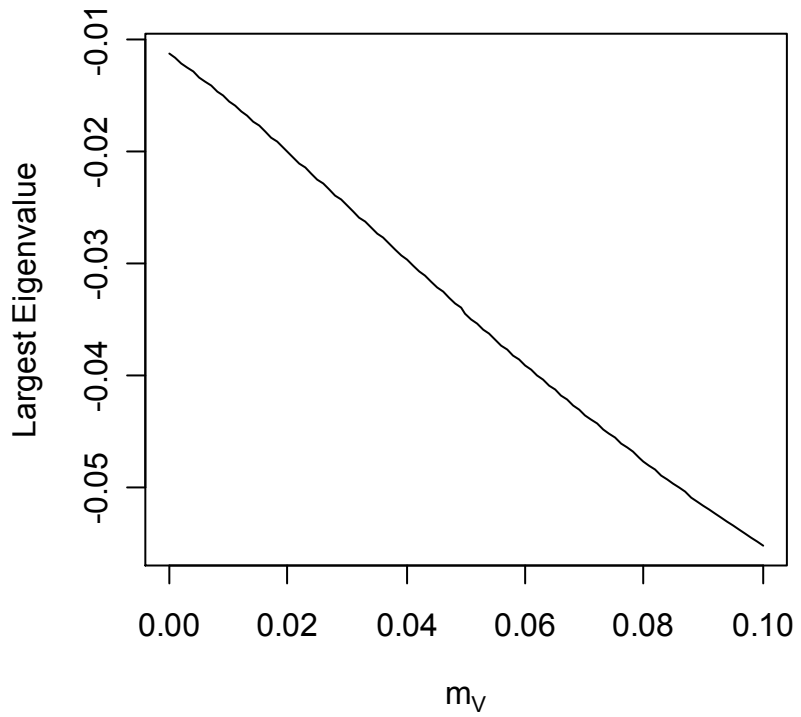
$$(38) \quad a_3 = \left( \begin{array}{l} \left( (-d_D - m_V) \frac{eI_{\max} P r - eI_{\max} 2rP^2}{E_h K + P K} - (-d_D - m_V) \frac{I_{\max} Z_S E_h}{(E_h + P)^2} \right) \\ - \frac{(-d_S d_D - d_S m_V + d_D m_V + m_V^2) r - 2rP}{K} - \frac{I_{\max}^2 Z_S P E_h e}{(E_h + P)^3} \\ + \frac{(-d_S d_D - d_S m_V + d_D m_V + m_V^2) I_{\max} Z_S E_h}{(E_h + P)^2} \\ - \left( (m_V^2) \frac{r - 2rP}{K} - (m_V^2) \frac{I_{\max} Z_S E_h}{(E_h + P)^2} \right) + \left( (d_D - m_V) \frac{I_{\max}^2 Z_S P E_h e}{(E_h + P)^3} \right) \end{array} \right)$$

From equations (36), (37), and (38), I was unable to find a condition for stability as a simple function of  $K$  or  $m_V$ .

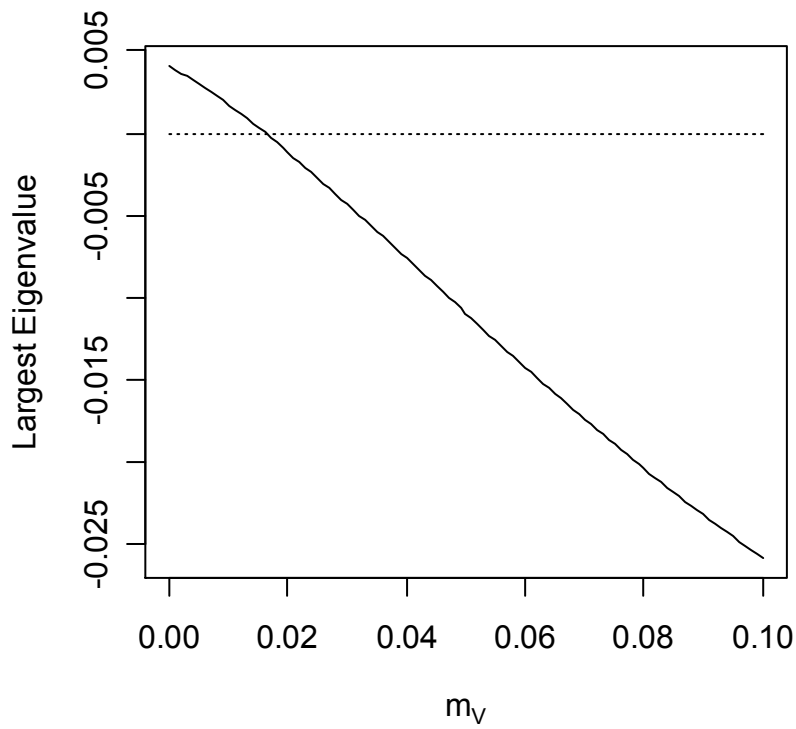




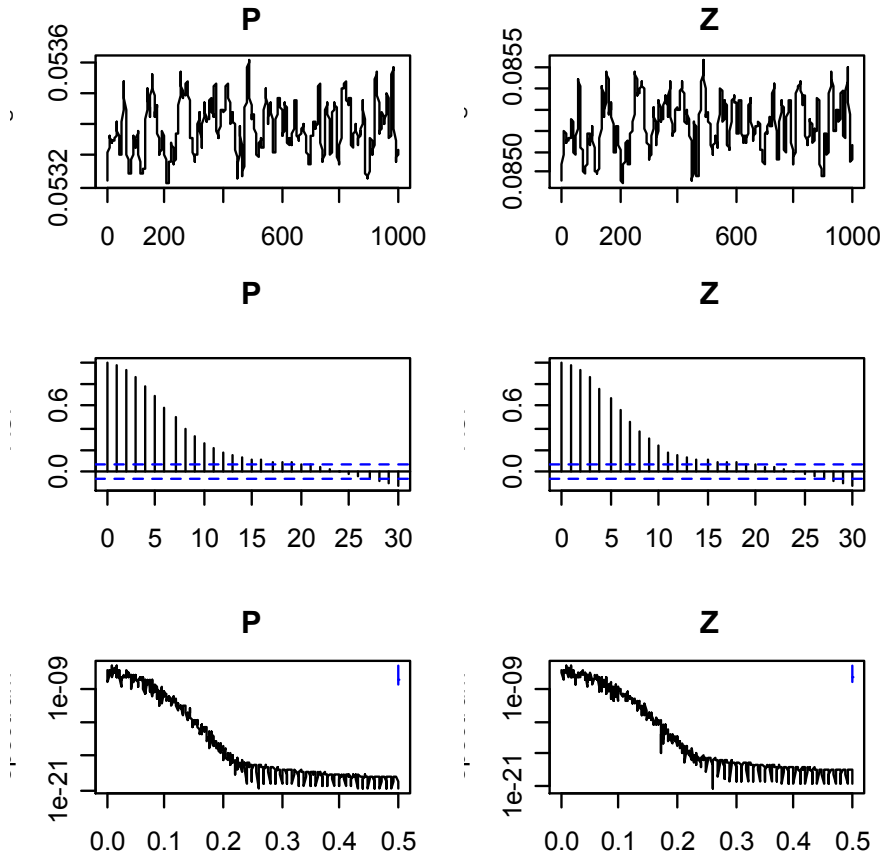
**Figure 2: Sample of a spectral slope plot. The solid line represents phytoplankton and the dotted line represents zooplankton. The dashed line down the middle is where the patch structure switches. To the left of the line, phytoplankton has a smaller patch scale. To the right of the line, zooplankton has a smaller patch scale.**



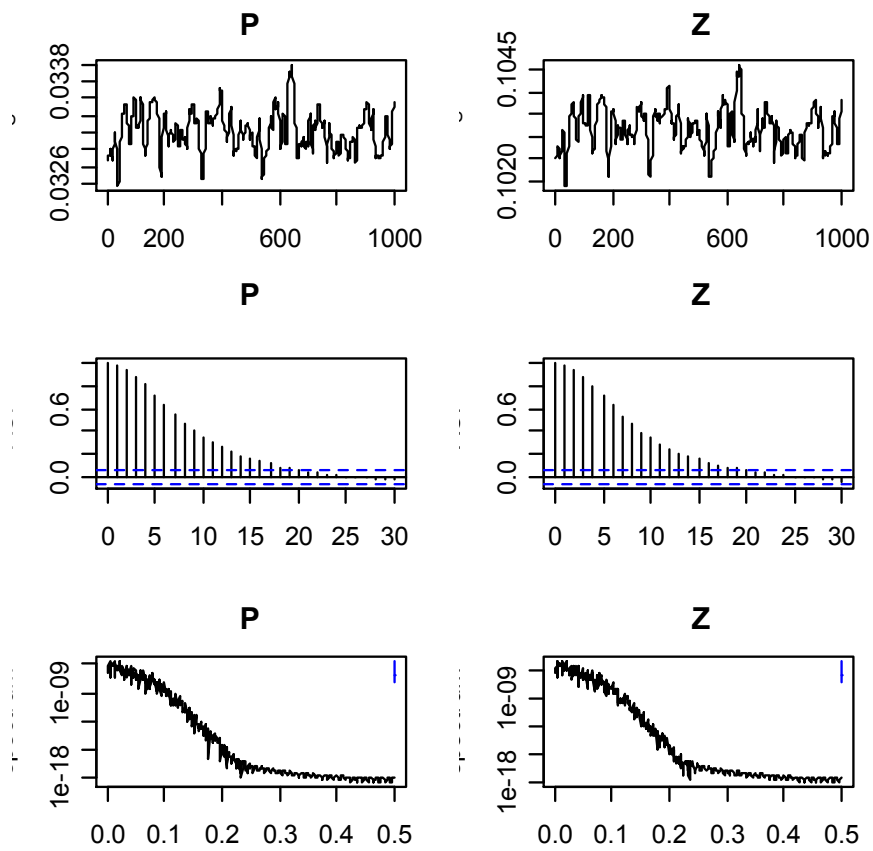
**Figure 3: Plot of the largest eigenvalue as vertical movement ( $m_v$ ) increases at the low value of  $K$  ( $K=0.22$ ). The solid line is the largest eigen value.**



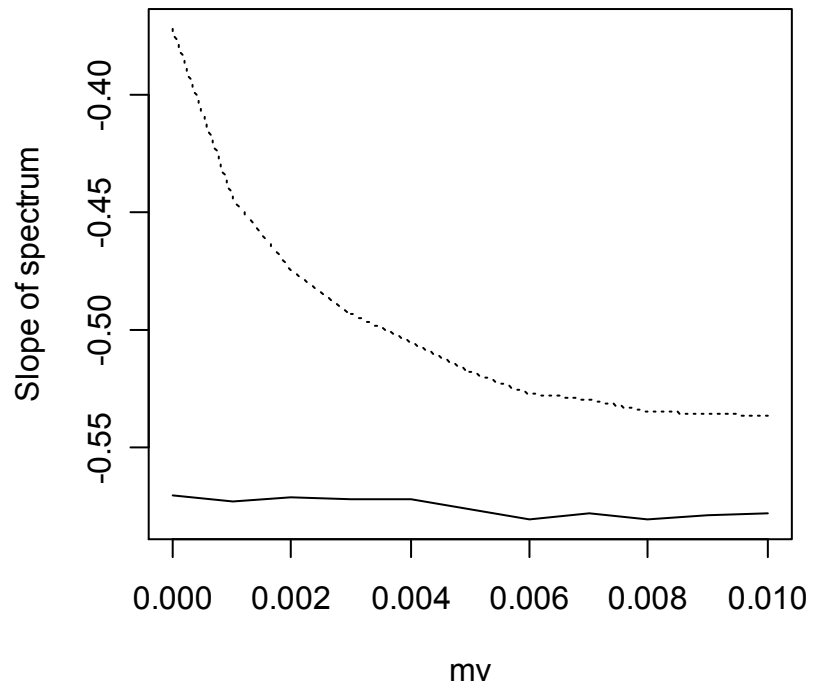
**Figure 4:** Plot of the largest eigenvalue as vertical movement ( $m_v$ ) increases at the high value of  $K$  ( $K=0.28$ ). The solid line is the largest eigen value and the dotted line is the zero line.



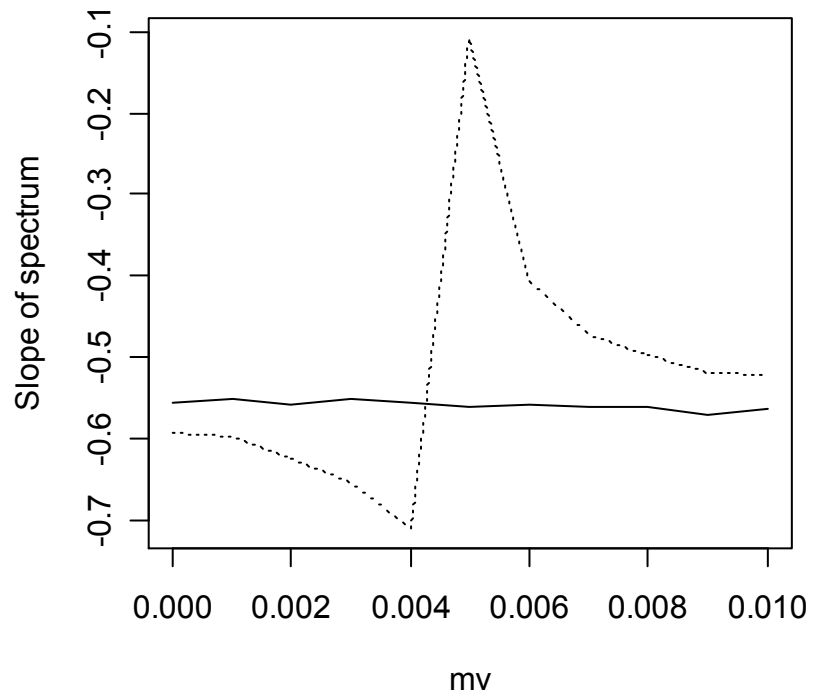
**Figure 5: Spatial distribution, autocorrelation, and spectra with data taken at low  $K$  ( $K=0.22$ ). All phytoplankton plots are on the left (labeled ‘P’ and all zooplankton plots are on the right (labeled ‘Z’). Series A are graphical representations of the population density (y-axis) across the number of compartments in my model (x-axis, total number =1000). Series B are the autocorrelation graphs. The y-axis is unitless (it is an indicator of the amount of correlation the population in one area has to itself in another area), with zero being no correlation and 1 being 100% correlation. The x-axis is the lag, measured in the same units as the movement rate. Series C are the spectra of the spatial arrangement of the plankton populations. Variance (between patches) is on the y-axis and frequency (1/distance between the compartments) is on the x-axis.**



**Figure 6: Spatial distribution, autocorrelation, and spectra with data taken at high  $K$  ( $K=0.28$ ). All other information (type of plot, axes, etc.) is similar to Figure 5.**



**Figure 7: Varying vertical movement ( $m_v$ ) at low  $K$  ( $K=0.22$ ). Solid line is phytoplankton, dotted line is zooplankton.**



**Figure 8: Varying vertical movement ( $m_v$ ) at high  $K$  ( $K=0.28$ ). Solid line is phytoplankton, dotted line is zooplankton.**

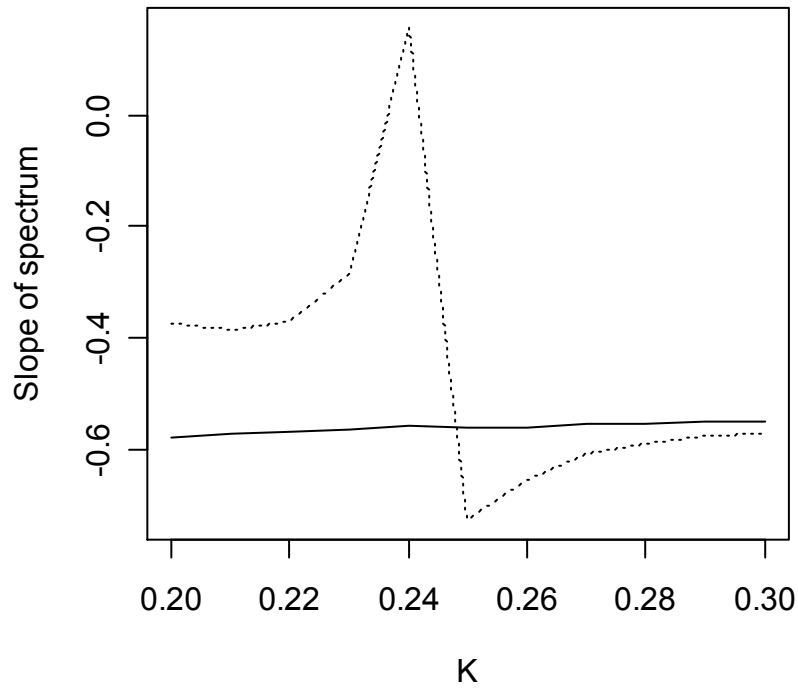
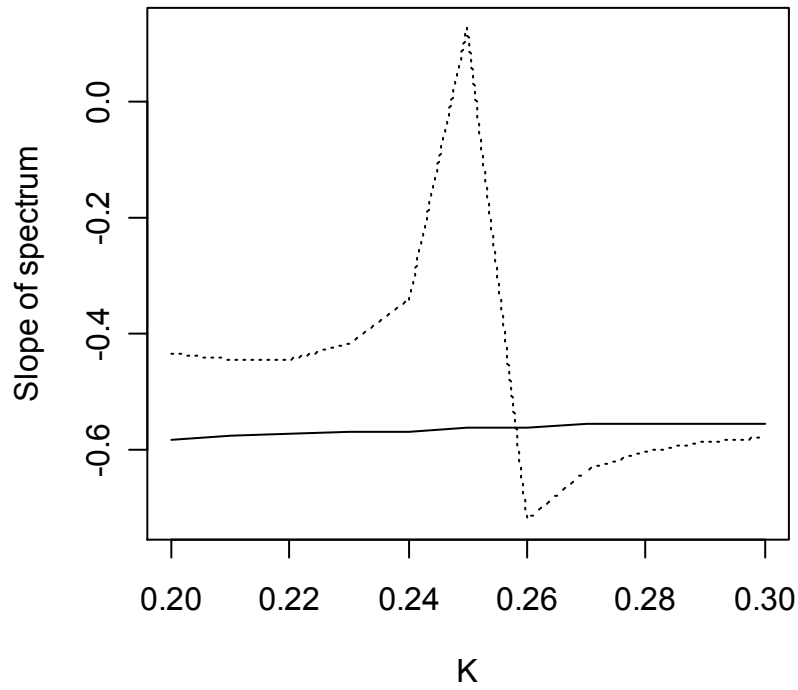


Figure 9: Varying  $K$  with no vertical movement ( $m_v=0$ ). The solid line is phytoplankton and the dashed line is zooplankton.





**Figure 10: Varying  $K$  with slow vertical movement ( $m_v = 0.001$ ). The solid line is phytoplankton and the dashed line is zooplankton.**

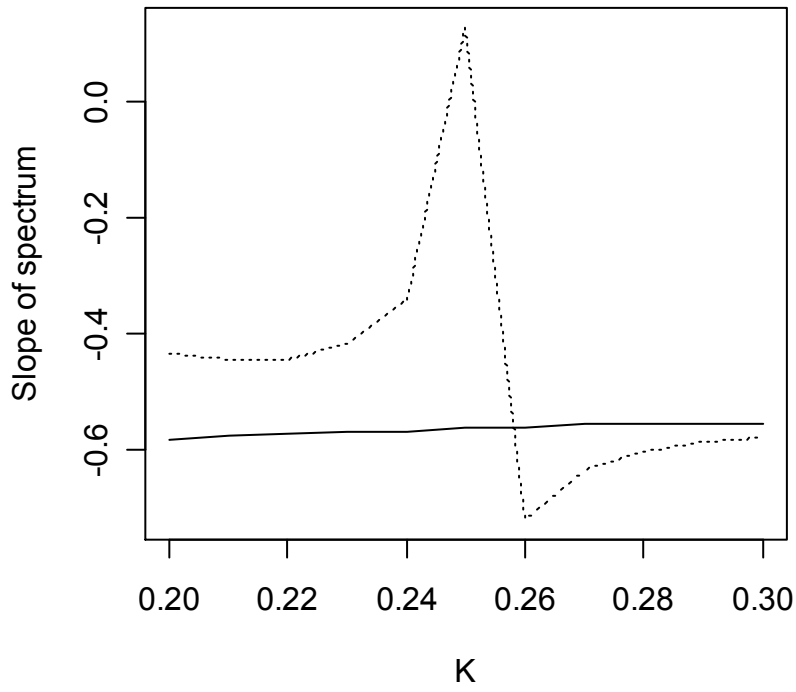


Figure 11: Varying  $K$  with fast vertical movement ( $m_v=0.01$ ). The solid line is phytoplankton and the dashed line is zooplankton.

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