MAINTENANCE OF DIVERSITY THROUGH
MULTIPLE TIMESCALES OF VARIATION

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I certify that I have read this thesis and that, in MY opinion, it is satisfactory in scope and quality as a thesis for the degree of Bachelor of Science in Global Environmental Science.

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For   Peter, Lisa, Patrick, and Julia Smith for always supporting me throughout my life and for many more years of love.

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ABSTRACT

Understanding the maintenance of diversity in phytoplankton is important because they are the base of the food web and they play a major part in biogeochemical cycles including the carbon cycle, which affects how the biosphere reacts to climate change. Diversity can be maintained through resource fluctuation because species can evolve different strategies to thrive under different conditions. These strategies include being able to grow the fastest, being able to store the most resources, or being able to use resources more efficiently, thus being the best competitor under limited resources. Nutrient supply in the ocean likely varies over multiple time scales (e.g., seasonal variation vs. storms); however, we do not understand how multiple frequencies of variation affects phytoplankton communities. To test the role of multiple frequencies of variation, I am using a model describing how phytoplankton respond to varying nutrient supply. I compared how the community structure during conditions where there were two pulse frequencies differ from communities under one-pulse frequency conditions.

Under one-pulse conditions it was reiterated that species with different strategies did better under competition at different periods. As the pulse periods increased there were clear shifts in the community structure with respect to the strategies. However, when a second pulse frequency was added, pulse periods where species with one strategy usually dominated, were found to contain a co-existence between species with multiple strategies. In short, it was found that multiple frequencies of resource variation allow for a greater diversity of strategies present in the community.

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CHAPTER 1

INTRODUCTION

One of the fundamental questions in ecology is: How is species diversity maintained?

This is an especially challenging question for diverse communities that use a small

magnitude of resources, such as phytoplankton, coral reefs, and forests (Petraitis et al.

1989). Diversity is one of the main components of ecosystem functionality, controlling

the magnitude an efficiency of an ecosystem, and as such, understanding how diversity is

maintained is important to understanding ecosystem processes (Chapin et al. 1997,

Cullen et al. 2002, Leps 2005). One overarching hypothesis for how diversity is

maintained has to do with variability in the input of resources into a system.  One study

(Armstrong & McGehee, 1980) outlines this used a model to show that diversity could be

maintained when species differ in performance between low and high resource levels.

This idea differs from the idea of diversity being maintained through competition and

niche development (Huston 1979). In aquatic systems nutrient limitation is very common

(Hecky & Kilham 1988, Moore et al. 2003, Edwards & Litchman 2014), however, there

are physical processes that create fluctuations in nutrient supply, such as upwelling,

seasonal cycling in higher latitudes, storms, fronts and eddies (Cullen et al. 2002,

Leichter et al. 2003, Levy et al. 2015). An example of fluctuations of resource supply in a

resource-limited terrestrial ecosystem can be found in one study (Chesson et al. 2004)

where it was determined that pulses of rain in a desert ecosystem allows for greater

diversity in desert plants. Resource fluctuation is important in a range of systems, and

here we will focus on phytoplankton as an important and relatively well-studied

community type.

Phytoplankton are the base of pelagic aquatic food chains. Therefore, understanding how populations are affected by changes in the physical environment is very important, especially considering the imminent threat of climate change (Leichter et al. 2003, Moore et al. 2003). Phytoplankton rely on the influx of nutrients to carry out their photosynthetic and biological processes. Phytoplankton have been shown to adopt different survival strategies for acquiring the nutrients needed to grow, and different strategies are better suited for different conditions. Three common strategies are: good competitive ability under a low concentration of nutrients, better storage capability under a transient increase in nutrients, and rapid growth under rich nutrient conditions (Sommer 1984). These strategies are determined by their quantitative score for three different traits: affinity for nutrient uptake, storage capacity, and maximum growth rate (Yamamoto & Hatta 2004, Edwards & Litchman 2014). These quantifiable strategies help explain how having different numerical values for three traits make a species better or worse at competition under different circumstances. It has been found that a trade-off arises in the three traits, meaning, in its simplest definition, one species cannot have the highest value for all three traits, and therefore one species cannot be the best at all three strategies (Sommer 1984; Gaedeke and Sommer 1986; Edwards et al. 2013).

The idea of resource fluctuation maintaining diversity has been investigated previously (Hay 1985, Gaedeke & Sommer 1986, Chesson 2000, Cullen et al. 2002), however those studies have only focused on a single timescale of resource fluctuation. This is problematic because in natural ecosystems there are multiple timescales and magnitudes of resource fluctuations occurring simultaneously. It is possible that having multiple frequencies of resource supply allows for greater diversity than a single

frequency, and that a greater difference between the timescales of the overlapping

frequencies will allow for more diversity. In this study, a model of competition and

coexistence under multiple timescales of resource fluctuation was analyzed. We used this

model to ask whether multiple timescales of fluctuation increases diversity relative to

single timescales of fluctuation. The model is parameterized for phytoplankton, but it is

relatively simple and the results are likely to apply to a broader range of ecosystems.

CHAPTER 2

METHODS

We aim to test whether multiple frequencies of resource supply alters diversity relative to a single frequency. We adapt a previously developed model (Grover 1991) of phytoplankton competition, which can model how they respond to variable resource supply.

2.1 Model Structure

The model is a system of ordinary differential equations, which are solved numerically using the deSolve R package (Soetaert et al. 2010). The following equations will be used:

$$\frac{dQ_i}{dt} = (V_{maxhi} - (V_{maxhi} - V_{maxlo,i})) \times \left(\frac{Q_i - Q_{\square in}}{Q_{max,i} - Q_{min}}\right) \times \left(\frac{R}{R+K_i}\right) - \mu_{\infty,i}\left(1 - \frac{Q_{min}}{Q_i}\right)Q_i \qquad (1)$$

$$\frac{dN_i}{dt} = \mu_{\infty,i}\left(1 - \frac{Q_{min}}{Q_i}\right)N_i - mN_i - aN_i \qquad (2)$$

$$\frac{dR}{dt} = a(S - R) - \Sigma_i\left(V_{maxhi} - (V_{maxhi} - V_{maxlo,i})\right) \times \left(\frac{Q_i - Q_{min}}{Q_{max,i} - Q_{min}}\right) \times \left(\frac{R}{R+K_i}\right) \times \left(\frac{N_i R}{R+K_i}\right) + \Sigma_i fmN_iQ_i \qquad (3)$$

The first equation describes the nutrient quota $Q$ for species $i$, which is the concentration of nutrients inside the cell at any given time (µmol P cell$^{-1}$), and which is gained through the uptake of nutrient from the environment and diluted through cell growth. The second equation describes change in biomass N (cell L$^{-1}$), which grows as a function of the nutrient quota, and is diminished through mortality and the mixing with deep water that causes a decrease in concentration. The third equation is nutrients in the environment R (µmol P L$^{-1}$), which are mixed into the surface ocean from deeper water, consumed by cells, and replenished through the recycling of dead matter.

The model was parameterized with values from previous experiments (Edwards et al. 2013) that reflect empirical values for phytoplankton limited by phosphorus.

Parameters that are constant across species include those for minimum phosphorous quota $Q_{min}$ (1.74 x $10^{-9}$ µmol P cell$^{-1}$), the highest value for maximum cell-specific phosphate uptake rate $V_{maxhi}$ (3.89 x $10^{-7}$ µmol P cell$^{-1}$ day$^{-1}$), and the mortality rate $m$ (0.01 $day^{-1}$). Environmental parameters include the rate at which phosphate mixes across the thermocline $a$ (0.1 $day^{-1}$), the fixed deep water concentration of phosphate $S$ (3 µmol L$^{-1}$), and the fraction of phytoplankton mortality that is recycled by decomposition in the mixed layer $f$ (0.7).

Studies have concluded that there is a trade-off between different strategies, allowing each species to either grow quickly under high phosphorus supply, store the most amount of phosphorus after a pulse, or compete better under limited phosphorus. The trade-off is dependent upon three parameters: the specific uptake affinity for phosphorus $P_{saff}$, the maximum growth rate $\mu_{\max}$, and the maximum phosphorus quota $Q_{max}$ (Edwards et al. 2013). In our model these parameters vary across species and are constrained by a three-way trade-off. In order to approximate a continuous plane of strategies, a matrix of trait values was created. Species can combine the strategies in different proportions to make them the best competitor under different circumstances. Species are assigned a value for $\mu_{\max}$ ranging between 0.2 and 3.5 day$^{-1}$, and a value for $P_{saff}$ ranging between $10^0$ and $10^6$ L µmol P$^{-1}$ day$^{-1}$. The three-way tradeoff is imposed by solving for $Q_{\max}$ as the third axis on the tradeoff plane: $\log_{10} Q_{max} = -5.77 - 1.22 \times \log_{10} P_{saff} - 5.91 \times \log_{10} \mu_{\max}$ (Edwards et al. 2013). These parameter values were used in the following equations to solve for the additional parameters $\mu_\infty$ and $V_{maxlo}$ :

$$\mu_\infty = \frac{\mu_{max} \times Q_{max}}{(Q_{max} - Q_{min})} \qquad (4)$$

$$V_{maxlo} = \mu_{\max} \times Q_{max} \qquad (5)$$

2.2 Multiple Pulses

Previous work (Litchman et al. 2009; Edwards et al. 2013) has shown that pulsed nutrient supply can allow multiple species to co-exist in this model under the appropriate trade-offs, but the number of surviving species is still small (about 2-4). We used the model to test if diversity changes when multiple time scales of variation occur at the same time, and we hypothesize that multiple time scales of pulsed nutrient supply will permit a greater number of species to coexist. Large pulse events are rarer (Turner and Dale 1998) and so a comparison will be made between frequent events of small magnitudes and rarer events of larger magnitude. During analysis of preliminary results, it was noticed that at intermediate periods (about $2^4$ days), there was a shift in the strategy that dominated in the communities. We implemented multiple pulse frequencies by varying the pulse period from $2^0$ to $2^8$ days, by powers of two, while simultaneously including a 'background' period of $2^2$, $2^4$, or $2^6$ days (Fig. 1). This allowed us to test the hypothesis that larger differences in period length would allow for greater community diversity.
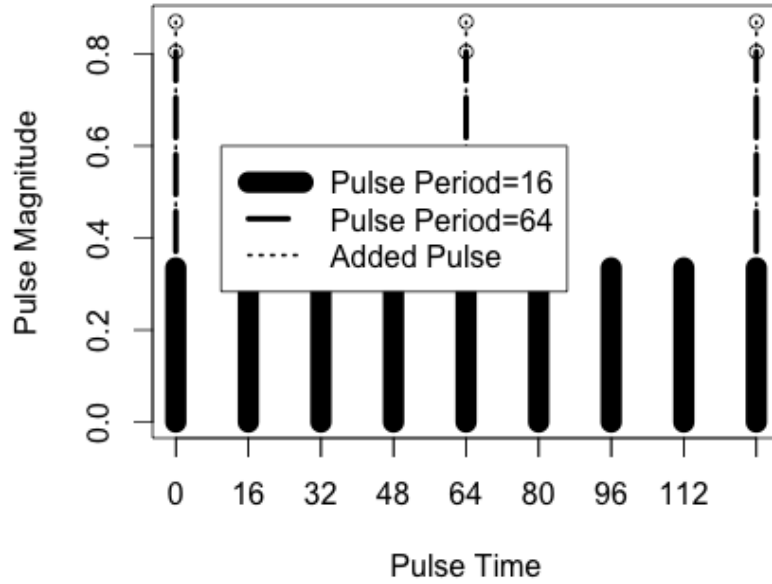
*Figure 1.* Figure shows how resources are added to the system in a pulse. The pulse times are the days at which pulses were input into the system. In this example the model was set with multiple timescales at 16 days and 64 days. The importance of this figure is to show how pulse magnitude relates to pulse period. Pulses coming in at more frequent time periods will have a smaller magnitude of nutrients to input.

Nutrient pulses were added to the model by replacing a fraction of the mixed layer with deep water. The magnitude for each pulse was created using the following equation $P_i = 1 - e^{-d \times T_i}$. The magnitude of the pulse $P$ is a function of the pulse period $T$ (days) and instantaneous mortality rate $d$ (day$^{-1}$). The pulse therefore removes a fraction of the biomass every $T$ days equivalent to the integrated mortality rate $d$ (0.0255 $day^{-1}$), in order to vary the frequency of nutrient pulses while holding integrated mortality and nutrient supply constant. Because each pulse period is paired with a pulse magnitude, during occasions when two pulse events coincide, the magnitude of the combined pulse was calculated to be $P_{1+2} = 1 - e^{-d \times (T_1 + T_2)}$ (Figure 1).
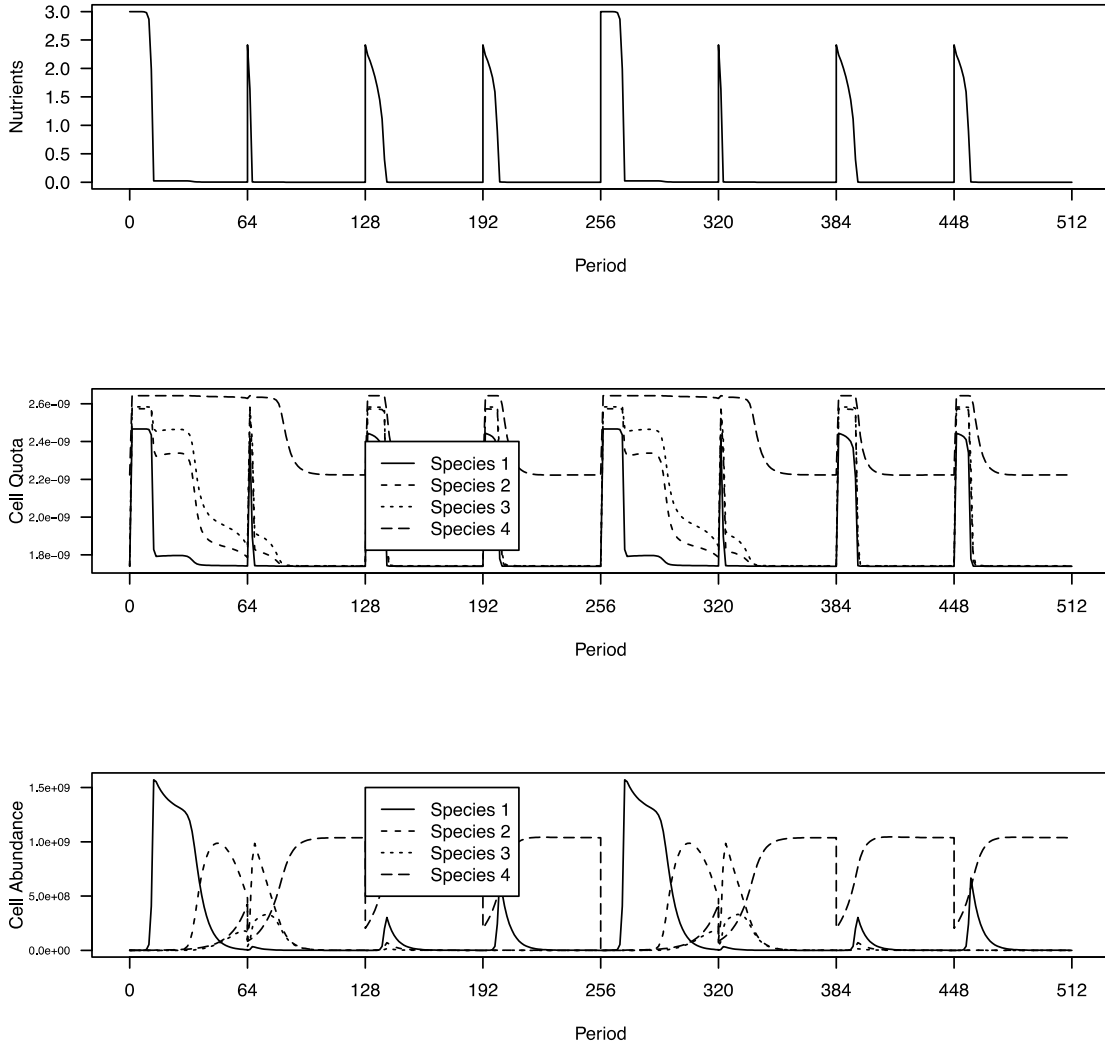
*Figure 2.* The dynamics of the competition while the model is running. In this example, the pulse periods were 256 and 64, which can be seen in the first panel labelled nutrients where a large pulse comes every 256 days and a smaller pulse comes every 64 days reiterating the relationship between period size magnitude size (Fig.1). In the second panel, which represent resources in the cell, shows how the resources in the cells vary over time. The final panel labelled cell abundance, shows the numbers of individuals for each species. The species labeled species 1 would be the species with the highest growth rate, because it grows the fastest when a large amount of nutrients becomes available, and the species labeled 4 would be the species with the highest affinity for nutrient uptake, because it does best under limited resources.

To simulate competition among many strategies, 400 different species were generated, with $\mu_{\max}$ ranging between 0.2 and 3.5 day$^{-1}$, $P_{saff}$ ranging between $10^0$ and $10^6$ L μmol P$^{-1}$ day$^{-1}$, and $Q_{\max}$ varying from $4.95 \times 10^{-17}$ μmol P cell$^{-1}$ to 0.023 μmol P cell$^{-1}$. Dynamics were simulated until they converged on a periodic

attractor (Figure 2). Species with very low abundance (a factor of $10^{-4}$ less than of the species with the highest abundance) were declared extinct and removed.

The model was run under several conditions to better understand the dynamics. These include: pulse magnitudes reduced by half; $Q_{max}$ held constant across species, while maintaining the tradeoff between $\mu_{max}$ and $P_{saff}$; and removal of nutrient recycling and mixing of nutrients into the system. Setting the nutrient pulses at half-magnitude allowed us to evaluate the fact that adding two frequencies of nutrient supply increases the total allotment of nutrients, and test whether the overall increase in nutrients affects the results. In order to understand how multiple frequencies of variation interacts with a simpler two-dimensional tradeoff, the model was run with $Q_{max}$ held constant across species at $2.00 \times 10^{-9}$ µmol P cell $^{-1}$. Finally, the model was run with the turbulent diffusion term ($a$) set to zero in order to simulate a set of conditions where there is no steady background flux of nutrients, and therefore the only supply of nutrients is through the pulse events. The recycling term ($f$) was also set to zero because recycling also results in a steady release of dissolve nutrients.
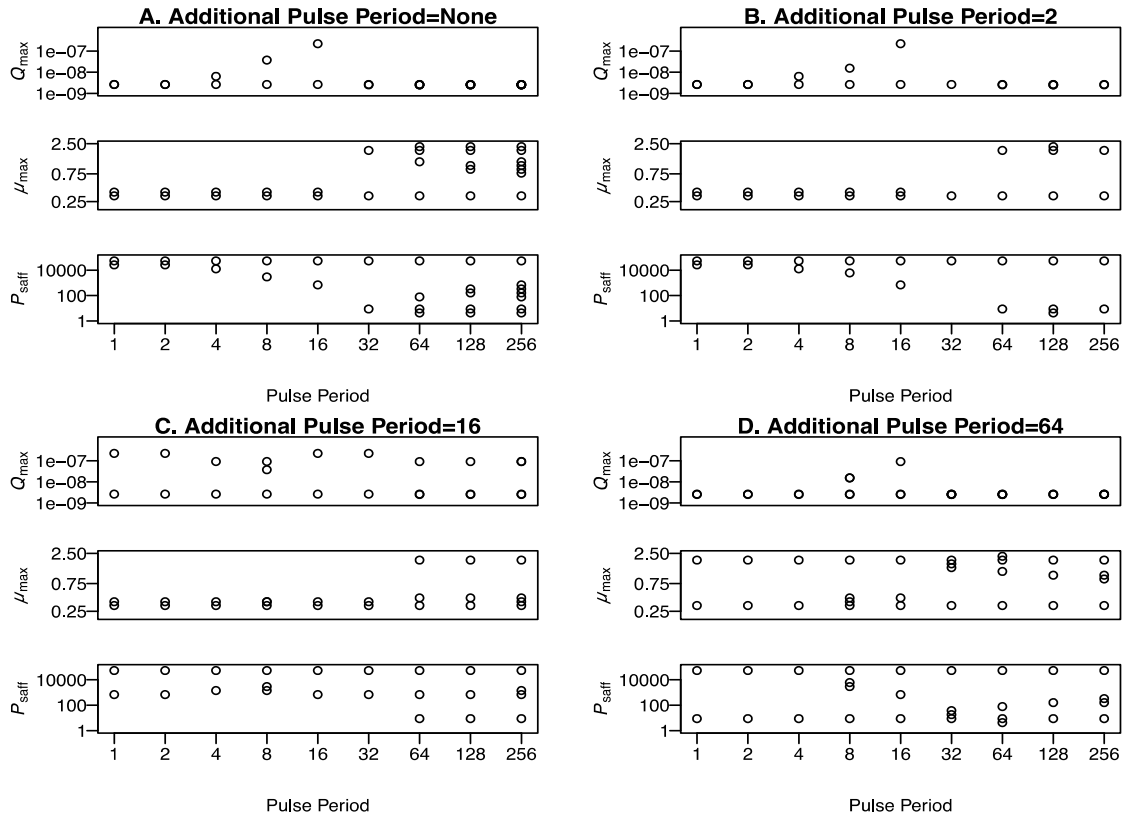
# RESULTS



*Figure 3.* Competition under one pulse frequency, and each of the following added frequencies: 2, 16, 64 days. The points represent a single species that won during that trial. For each day, the value for each trait that the winning species had is plotted. These graphs are to be read first vertically (per panel), comparing each trait value at each period, then read horizontally, comparing the trends, i.e. the changes in the population structure, i.e. the trait values that dominate in the population, over time.

## 3.1 One frequency of pulsed nutrient supply

Under a single frequency of pulsed nutrient supply, community structure varied as found previously (Edwards et al. 2013), which we review here. Across a gradient of pulse frequencies, there were clear differences in which strategies persisted. Under pulse periods of 1 and 2 days the species with the highest affinity for phosphorous uptake were prevalent, and there was no co-existence of other species/strategies (Fig. 3A). At a pulse period of 4 days, a species with a higher storage capacity ($Q_{max}$) and a lower affinity for phosphorus can coexist with a higher affinity strategy. Between pulse periods of 4 to 16 days there was coexistence between species with high affinity for phosphorus uptake and species with large storage capacities, and the species with the high storage capacity value has a value of $Q_{max}$ that increases as the pulse period increases (Fig. 3A). Under these conditions, while the storage strategy is persisting the maximum growth rates ($\mu_{max}$) of the community are consistently low. When the pulse period increases to 32 days, the community shifts such that storage capacity of all species takes on a minimum value, while a species with high maximum growth rate can now coexist. For pulse periods of 64 to 256 days, there is an emergence of species with intermediate $\mu_{max}$ and affinity values, while all the species' $Q_{max}$ values are still at the minimum. Throughout all pulse frequencies, there is one species with high affinity for phosphorus that persists.

3.2 Two frequencies of pulsed nutrient supply

When nutrients were delivered in pulses at two different frequencies, this primarily resulted in the coexistence of strategies adapted to those frequencies, based on the single-frequency results (Fig. 3A), as well as other community shifts. We will describe how community structure changes with pulse frequency, under different

'background' frequencies that are simultaneously present. With a background pulse period of 2 days, community structure showed similar trends to the single-frequency results, up to a pulse period of 16 days (Fig. 3B). A species with high $\mu_{max}$ does not appear under a pulse period of 32 days, in contrast to the single-frequency results. In addition, under the longer pulse periods there are fewer species with intermediate $\mu_{max}$ and $P_{saff}$ values (Fig. 3B). When a background pulse frequency of 16 days is added (Fig. 3C), species with high $Q_{max}$ and intermediate $P_{saff}$ values appear under shorter periods, compared to a single pulse frequency, and they persist throughout all periods. A species with high $\mu_{max}$ and low $P_{saff}$ does not appear until a pulse period of 64 days, while under a single pulse frequency this species appeared at a pulse period of 32 days. There is also a loss of species with intermediate $\mu_{max}$ and $P_{saff}$ under the longer pulse periods. These species are replaced by the persisting species with high $Q_{max}$ and intermediate $P_{saff}$ values. Finally, when the background pulse frequency is 64 days (Fig. 3D), species with high $\mu_{max}$ and low $P_{saff}$ values persist throughout all pulse periods, while under a single pulse frequency they would only be present at longer pulse periods. The emergence of species with increasing $Q_{max}$ begins when the pulse period is 8 days, rather than at 4 days, but the same pattern of the loss of species with high $Q_{max}$ at a pulse period of 32 days is still seen.
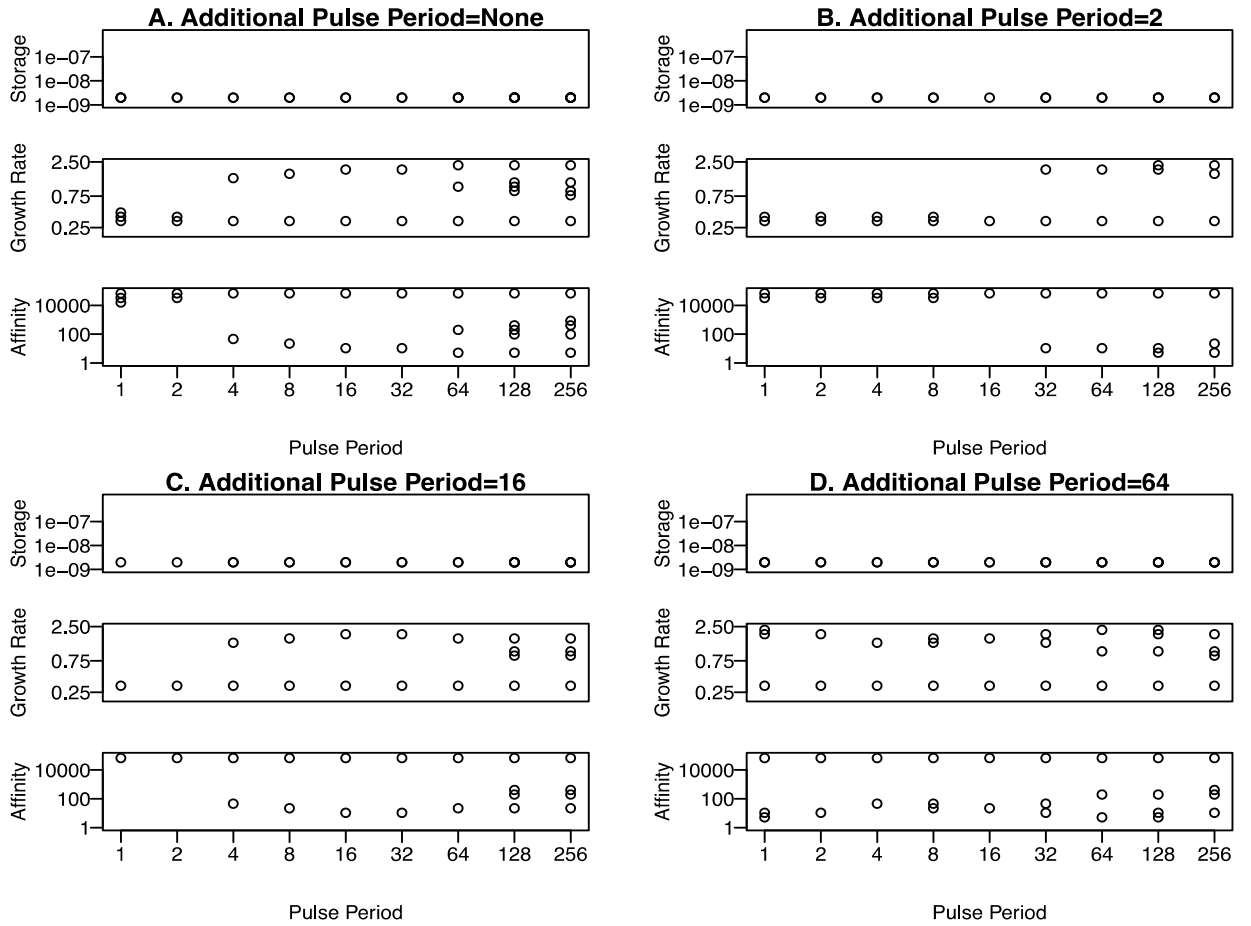
## 3.3 Two-way tradeoff: Constant Q$_{max}$



*Figure 4.* Competition under one pulse frequency, and each of the following added frequencies: 2, 16, 64 days when the trait value for maximum storage capacity is set to a constant value for all species. The points represent a single species that won during that trial. For each day, the value for each trait that the winning species had is plotted. These graphs are to be read first vertically (per panel), comparing each trait value at each period, then read horizontally,

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comparing the trends, i.e. the changes in the population structure, i.e. the trait values that dominate in the population, over time.

We also analyzed the model with $Q_{max}$ held constant across species, to explore how community structure is affected by multiple frequencies of nutrient supply when a simpler tradeoff constrains trait variation. Holding $Q_{max}$ constant under one pulse frequency allows for a species with high $\mu_{max}$ and low $P_{saff}$ to persist in all periods, except when the pulse period is 1 or 2 days (Fig. 4). In the longest three pulse periods (64, 128, and 265 days), species with intermediate $P_{saff}$ and $\mu_{max}$ values appear alongside the species with the highest $\mu_{max}$. When a background pulse frequency of 2 days is added (Fig. 4B), there are two species with high $P_{saff}$ and low $\mu_{max}$ that coexist until the pulse period is 8 days. After this, the species with the highest $P_{saff}$ and lowest $\mu_{max}$ persists, but the second species is replaced with one that has high $\mu_{max}$ and low $P_{saff}$. When a background pulse frequency of 16 days is overlaid (Fig. 3C), there is a species with high $P_{saff}$ and low $\mu_{max}$ that appears throughout all the pulse periods. However, when the pulse period is 4 days, a species with an intermediate value for $\mu_{max}$ persists, and at a pulse period of 8 days this is replaced by a species with a slightly higher $\mu_{max}$. This pattern is seen until the pulse period is 16 days, and then the species with the highest $\mu_{max}$ is replaced by a species with a slightly lower $\mu_{max}$. The species that persists when the pulse period is 64 is the same species that persisted when the pulse period was 8 days. This species persists through the two longest pulse periods, and coexists with two species with intermediate values of $\mu_{max}$ and $P_{saff}$. With a background period of 64 days (Fig. 4D), a species with high $P_{saff}$ and low $\mu_{max}$ persists in all pulse periods, and coexists with one or two species with intermediate to high $\mu_{max}$.

3.4 Reduced pulse magnitude

Halving the magnitude of the nutrient pulses caused only minor shifts in the patterns of community structure already described (Supplementary Figure).

3.5 Removal of continuous nutrient supply

When continuous nutrient supply through mixing and recycling were removed, this caused extinction of the species with high $P_{saff}$ that was present under all other conditions (Supplementary Figure). Otherwise, patterns of community structure were similar to the results already described.
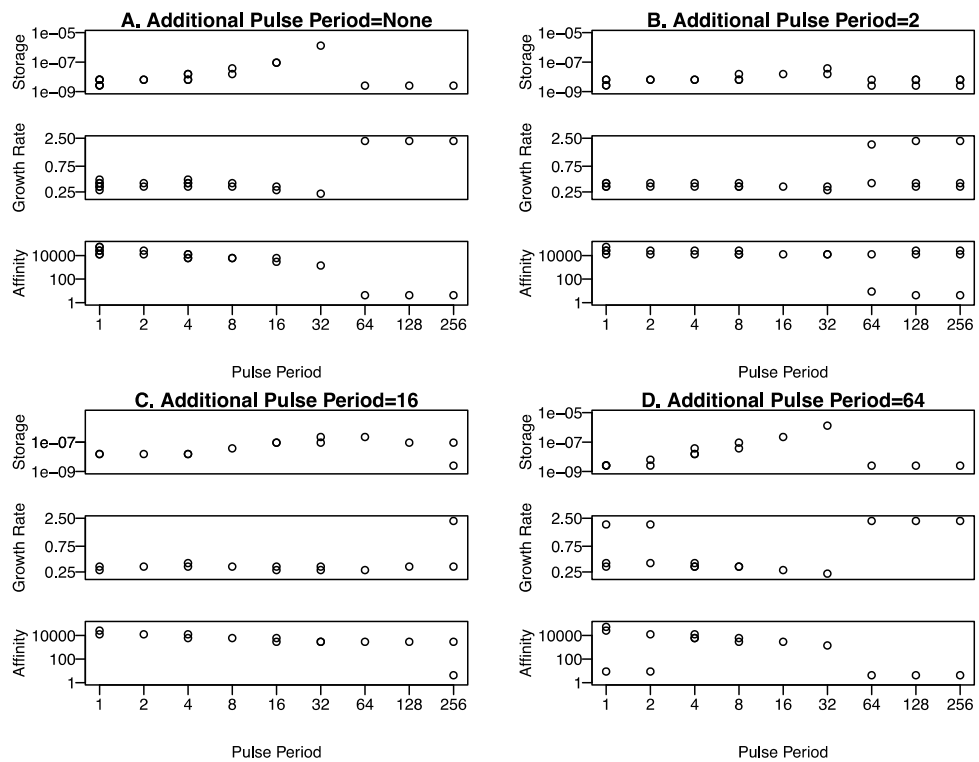
*Figure 5.* Competition under one pulse frequency, and each of the following added frequencies: 2, 16, 64 days, when the terms for recycling and diffusion of nutrient in the model is set to zero. The points represent a single species that won during that trial. For each day, the value for each trait that the winning species had is plotted. These graphs are to be read first vertically (per panel), comparing each trait value at each period, then read horizontally, comparing the trends, i.e. the changes in the population structure, i.e. the trait values that dominate in the population, over time.

CHAPTER 4

DISCUSSION

4.1 Effects of multiple frequencies of nutrient supply

As shown previously, under a single frequency of nutrient supply, changing the

period/magnitude of the pulse causes large shifts in community structure, with multiple

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strategies often coexisting. When pulse periods are small, every day or two, the dominant strategy is affinity. Because these periods are short and only deliver a small amount of nutrients, it is almost as if there is a steady stream of nutrients. Therefore, it is advantageous to have high uptake rates for low concentration of nutrients. For periods of 4-16 days, the time between pulses is great enough that a strategy of storing nutrients can now persist as well. The advantage of storing nutrients declines under longer pulse periods, because the amount of time between nutrient introductions is so long that stored nutrients are exhausted during growth. Therefore, it becomes advantageous to instead grow as fast as possible while the nutrients are available. Thus there is a shift toward the final strategy of maximizing the maximum growth rate.

We initially expected that incorporating multiple pulse frequencies would cause an overall increase in the number of species able to coexist. However, there was no clear difference in the number of species able to coexist between one pulse frequency and two pulse frequencies (usually 2-3 species, sometimes 4-5). Instead, what differed was the functional diversity of strategies that coexist. With one frequency, as discussed, there was clearly pulse periods where the coexisting species had distinct strategies, and there are clear shifts between these strategies across conditions. With two frequencies, the coexisting community is in some ways the sum of the communities that emerge under each individual frequency. Pulse periods of ~1-2 weeks favor species with high $Q_{max}$, and pulse periods > 1 month favor species with high $\mu_{max}$. When frequencies in both of these ranges are present, both strategies occur (Fig. 3). In addition, species with high $P_{saff}$ can occur under all conditions, which is discussed further below. However, the idea that two frequencies results in adding together two coexisting communities is not entirely correct.

For example, under the longest pulse periods species with intermediate µmax can coexist with high $\mu_{max}$ and high $P_{saff}$ species (Fig. 3A), but when a pulse period of 16 days is added a high $Q_{max}$ species is added and appears to exclude the intermediate $\mu_{max}$ species.

The way that this model was designed actually creates three different inputs of nutrients at three different frequencies: the first pulse frequency, the second pulse frequency, and the mixing and recycling that acts as a constant influx of nutrients into the system. When mixing and recycling were turned off, the species with high $P_{saff}$, which previously persisted under all conditions, disappeared. This is likely because this strategy is the best competitor during the periods between pulses when nutrient concentrations are low. Therefore, the persistence of this species is another example of how species with different strategies can co-exist when different supply frequencies selecting for those strategies are combined. When mixing and recycling were turned off, the low but steady nutrient input was removed, and therefore the species best adapted to this mode of nutrient supply were not able to survive.

## 4.2 Implications

Although our model is parameterized for phytoplankton limited by phosphate, the structure of the model is relatively simple, and therefore the results may apply to a broad range of systems where resources vary over time. This model is parameterized for phosphorus due to the amount of data on the relevant tradeoffs, however similar dynamics could operate for nitrogen, which is often limiting in the ocean as well as lakes

(Litchman et al. 2009). It has been previously found (Litchman er al. 2009, Edwards et al. 2012) that affinity for nitrogen intake and $Q_{max}$ for nitrogen vary across species, similar to phosphorous, and therefore similar tradeoffs may operate for nitrogen.

Our results may also be relevant for other types of systems, such as arid or forest plant communities. In arid environments, the frequency of rainfall events has an effect on plant diversity. Rain events of small magnitude are common in arid and semi-arid environments, with medium-sized events that occur less frequently, and large events that are highly variable (Schwinning & Sala 2004). These events are similar to the pulses of phosphorus in our model, where there are smaller more frequent events and larger less frequent events. In arid environments, water is distributed to the plants based on soil infiltration. When there are smaller events the water only reaches the top soil, and therefore species who have shorter roots are able to utilize the added resource. Species who have deep roots would thrive during times when there are large events that give the water time to penetrate the soil deeper (Chesson et al. 2004). It was found that single rainfall events can trigger increases in photosynthetic rates in some plants, but not in all. In one rain event with soil penetration depth of 5 mm, one species of grass flourished, however plants with deeper roots were not affected (Schwinning & Sala 2004). Biodiversity in arid environments could possibly be maintained through the pairing of high frequency and low frequency rainfall events.

Another significant resource that could experience similar community dynamics is space. Spatial competition can be common in terrestrial and marine intertidal communities. In terrestrial environments, fires and droughts can be an important source of disturbance to which some species are well-adapted. For example, Guinea grass has

the ability to withstand fires and therefore when a fire occurs, can quickly spread into the holes left from other species (Rojas-Sandoval & Acevedo Rodriguez, 2013). Fires spark succession in the plant community, leading to distinct temporal dynamics of species that can grow and occupy space the fastest, and hardier plants that can survive in the altered soil and eventually weed out the primary successor (Connell & Slatyer 1977). Furthermore, there are tertiary successors, which are species widespread in the area that outcompete the secondary successors. If there are multiple frequencies of fire events (of different magnitude), there could be a mixture of all three succession types in the landscape. In rocky intertidal environments space can be an important limiting factor as well. One study (Souza 1979) found that the frequency at which boulders in a rocky tidal area were disturbed is what maintained the diversity of algal species. Small boulders that are frequently disturbed only have a short window of time for colonization of the opened space, therefore favoring species with the highest abundances at the time of disturbance. Larger boulders that get disturbed less frequently were also found to be limited in species diversity, usually overwhelmingly dominated by one species of algae. However, there was the most diversity on intermediate sized rocks that have intermediate disturbance frequencies. The smaller boulders turn over too frequently, and the larger boulder does not turn over and create open space frequently enough for wide ranges of species. The intermediate sized rocks do not kill the majority of the species when it turns over, like the large boulders, and is not constantly being turned over, giving species time to settle and grow in population.

4.3 Future Direction

The next step would be to turn to the lab to test the validity of the model. Like the model, no one has tested the effects of multiple frequencies of resource input on phytoplankton communities in the lab. Several experiments have shown that pulsed nutrient supply can promote diversity in the lab (Sommer 1984), but the role of multiple frequencies has not been tested. In addition, another future direction is to relate the results found here to new work that uses high resolution physical models to explore how plankton communities respond to realistic environmental variability (Levy et al. 2015).
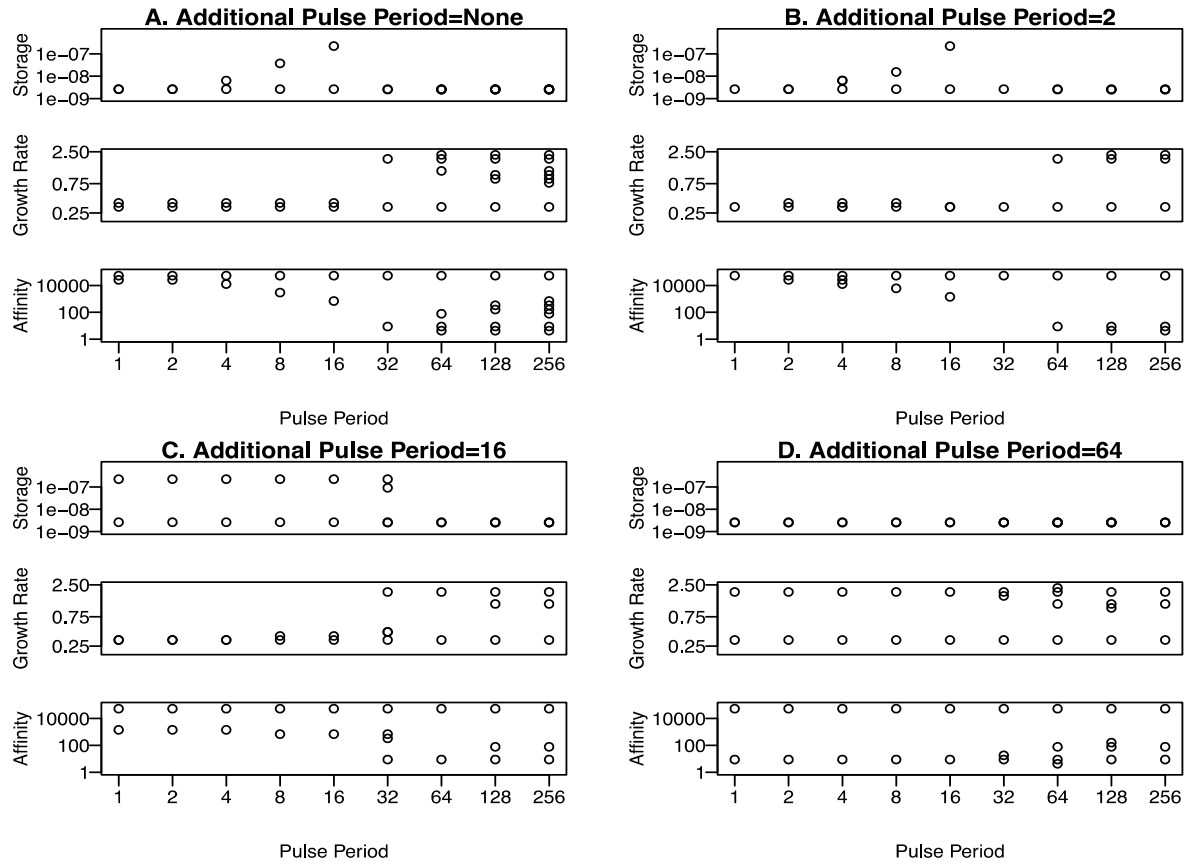
*Figure 6.* Competition under one pulse frequency, and each of the following added frequencies: 2, 16, 64 days, when the magnitude of the pulses is reduced by half. The points represent a single species that won during that trial. For each day, the value for each trait that the winning species had is plotted. These graphs are to be read first vertically (per panel), comparing each trait value at each period, then read horizontally, comparing the trends, i.e. the changes in the population structure, i.e. the trait values that dominate in the population, over time.

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