A System of Difference Equations model for Harmful Algal Bloom causative organism

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ABSTRACT

The dinoflagellate *Pyrodinium bahamense* var. *compressum* has been known to be the major cause of harmful algal blooms or H.A.B. recurring in Manila Bay and other bodies of water in the Philippines. This paper proposes a system of difference equations to describe the population dynamics of the different life cycle stages of this dinoflagellate. Initial numerical results show that the model reasonably captures the population dynamics shown in nature.

1. INTRODUCTION

1.1 Rationale

Pyrodinium bahamense var. *compressum* has been known to cause major problems concerning health and economy in the Southeast Asian region. Cysts of P. bahamense are currently mainly found in the Southeast Asian region, with blooms being reported in Malaysia, Indonesia, and the Philippines. These algal blooms have caused a lot of casualties. For example, in the red tide that occurred in Manila Bay in 1988, the seafood industry suffered a loss of about USD 300,000/day [1]. Cases of Paralytic Shellfish Poisoning related to P. bahamense var. compressum reached to around 3101 cases, 1995 of which are from the Philippines alone [1].

The life cycle of *P. bahamense* (refer to Figure 1) mainly consists of three stages : the resting cyst, the vegetative cell, and the floating cyst. While there is a clear process of its life cycle, there are still unknown factors that can affect it. For example, it still remains a mystery as to why a vegetative cell would choose to enter the floating cyst stage instead of the resting cyst stage.

1.2 Modeling Attempts

Novel features of the Pyrodinium lifecycle such as the mandatory rest period of 3-4 months [11] would limit the application of traditional models based on Ordinary Differential Equations(ODEs) to the organism. Individual Based Models(also known as *Agent Based Models*) have been gaining widespread usage in phytoplankton modeling : not only would ABMs capture novel life cycle features or stages that would otherwise be missed by generic ODE models, they could also potentially elucidate dynamics that arise from the interactions of, and variations among, the population members being studied.

A major drawback of ABMs is the intensive computing power and time that they require. Depending on the population size modeled(which could reach to the millions in a HAB study), the computing power required could become inconvenient, if not outright prohibitive.

In this work, a system of Difference Equations was used as a "middle way" measure between ODEs and ABMs. The ease with which they could be manipulated and represented as discrete data structures(particularly arrays) enabled the modeling of novel Pyrodinium life cycle features(such as the mandatory resting period) and population events(such as instantaneous death of vegetative cells due to starvation), both of which would be missed by ODEs. All insights that could be derived from system of Difference Equations could also be derived from ABMs : while more "individualistic" than the inherently Eulerian ODEs, the capabilities of system of Difference Equations are still limited compared to ABMs. Nevertheless, for comparable population sizes being simulated, the computing time required for system of Difference Equations are orders of magnitude than that for ABMs, making them still potentially useful and insightful as modeling tools.

Villanoy et al[5] modeled a single bloom of Pyrodinium Bahamense in Manila Bay using an ABM. Combined with hydrodynamic wave models, they modeled how a bloom could spread to the different portions of the bay from a single point source during a bloom incident. Since their

simulations spanned 16 days, the effect of sexual reproduction in the creation of an innoculum for subsequent blooms was no longer covered, as well as the effect of the mandatory resting period[11] in those blooms.

This work, in comparison, utilizes a system of Difference Equations and takes into account the mandatory resting period. The periods simulated spanned multiple years, and the effect of bloom-end events in innoculum production for subsequent blooms was also explored. While Villanoy et al[5], explicitly initiated a bloom at the beginning of the simulation, in our model, blooms are triggered(ended) by the presence(absence) of nutrients.

2. P. BAHAMENSE VAR. COMPRESSUM LIFECYCLE

While there are still gaps in the knowledge of *P. bahamense* var. *compressum* lifecycle [12, 8, 9], the increased availability of laboratory cultures have resulted in a more extensive description of its life cycle [10].
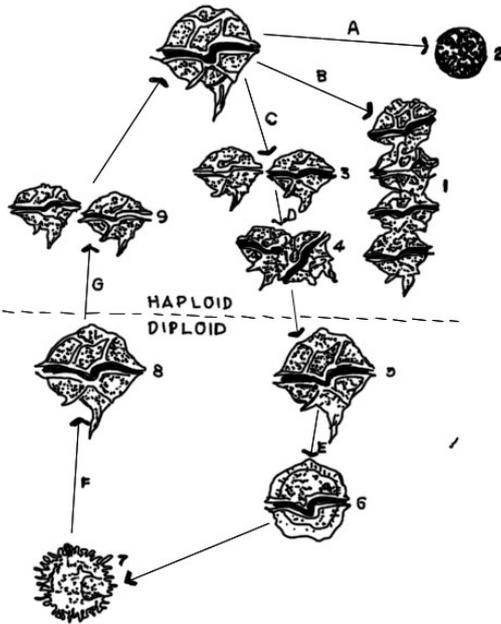

Figure 1: Life Cycle Diagram

P. bahamense perform cell division (binary fission) of their haploid (N) vegetative stage, which forms the "blooms" in the water column [3]. Field samples from Oyster Bay, Jamaica and Papua New Guinea show that cell division occurs roughly about every 2.5 days [4, 7].

Near the end of the "blooms"–when nutrient levels are lower [11]– the vegetative cells form a planozygote (2N) through union of gametes [3]. During the resting cyst stage, there is a mandatory resting period of 3-4 months before they can return to the vegetative stage [6]. If during the vegetative stage the conditions are not conducive to growth, then the cells turn to temporary cysts [3]. These cysts can return to the vegetative stage when conditions become favorable, at which the cell resumes division [13]. It is yet unknown what factors cause the vegetative cells to turn to resting cysts instead of temporary cysts [13].

3. EQUATIONAL MODEL

As previously mentioned, an equational model was used to model three stages of *P. bahamense*. The equational model itself consists of four main equations, three of which represent one stage of the lifecycle, and one representing the nutrients available. However, there are also additional equations that represent important factors for the cell, such as nutrition consumption.

3.1 Coefficients

Before we discuss the modeling equations, we first define the coefficients used in forming them.

a) α- encystment rate. It refers to the rate at which a portion of the population turn into a cyst.

b) Excystment rates. They refers to the rate at which a portion of the population turn into vegetative cells. There are two types of excystment for this model : excystment of a resting cyst to vegetative cell, denoted as γ_1, and excystment of a floating cyst to vegetative cell, denoted as γ_2.

c) κ- fission rate. It refers to the rate at which vegetative cells multiply via binary fission.

d) μ is the percentage of the population that undergoes sexual reproduction at a given time.

e) φ is the percentage of the population that undergoes asexual reproduction at a given time.

f) ω denotes the number of children a cell produces under sexual reproduction. Note that this does not mean that a cell only produces this amount during its lifespan, it simply means that it only produces this amount at a given time.

g) ϑ is a value that denotes the length of a cell's life. The assumption here is that a cell dies after a number of days.

h) ς is the value that denotes the length of the resting cysts' mandatory resting period.

Additionally, we have a binary function ψ that returns either 1 or 0, depending on the number of nutrients available. We define it as follows :

$$\psi(t) = \begin{cases} 1, & K(t) > 0 \\ 0, & \text{otherwise,} \end{cases}$$

where $K(t)$ is the amount of nutrients in the system present at time t, and whose dynamics is discussed below.

3.2 Difference Equations

Four difference equations comprise our model, three of which represent the three stages of the life cycle. The last one represents the nutrient component which we assume to play an important role in the interplay.

3.2.1 Resting Cyst

For the resting cyst, we have the following :

$$\begin{cases} \dfrac{\Delta R(t)}{\Delta t} &= \mu \cdot \omega \cdot V(t) - \gamma_1 \cdot \psi(t) \cdot C(t) \\ R(t) &\geq 0, \end{cases} \quad (1)$$

where $R(t)$ is the population at time t; $\gamma_1 \cdot \psi(t) \cdot C(t)$ is the amount of cysts that become cells at this time; and $\mu \cdot \omega \cdot V(t)$ is the number of vegetative cells that turn into resting cysts, modified by the number of offspring that it can have and the sexual reproduction rate.

$C(t)$ is a function that represents the number of cysts that are viable to become cells. Resting cysts have a mandatory

resting period, where they are unable to become cells. However, they do not immediately turn into cells after this period. Thus, it is possible to remain as cysts for a longer period of time than the mandatory resting period. $C(t)$ is defined as :

$$\frac{\Delta C(t)}{\Delta t} = \mu \cdot \omega \cdot V(t - \varsigma) + (1 - \gamma_1 \cdot \psi(t)) \cdot C(t). \quad (2)$$

The first term on the right-hand side reflects the idea that the "new cysts" only become viable to become cells after the mandatory resting period. On the other hand, the second term simply states that the viable cysts that do not become cells today are still viable for the next day.

3.2.2 Vegetative Cell
The differential equation for the vegetative cell is defined as :

$$\begin{cases} \begin{aligned} \frac{\Delta V(t)}{\Delta t} & = \kappa \cdot \varphi \cdot V(t) - \Theta(t) \\ & \quad + 2\gamma_1 \cdot \psi(t) \cdot C(t) - \alpha \cdot \psi(t) \cdot V(t) \\ & \quad + \gamma_2 \cdot \psi(t) \cdot F(t), \\ V(t) & \geq 0, \end{aligned} \end{cases} \quad (3)$$

where $\kappa \cdot \varphi \cdot V(t)$ is the number of vegetative cells that multiply via binary fission, affected by the rate of asexual reproduction ; $2\gamma_1 \cdot \psi(t) \cdot C(t)$ is the number of resting cysts that turn into vegetative cells ; $\alpha \cdot \psi(t) \cdot V(t)$ is the number of vegetative cells that turn into floating cysts ; $\gamma_2 \cdot \psi(t) \cdot F(t)$ is the number of floating cysts that turn into vegetative cells ; and $\Theta(t)$ is the number of cells that die at time t. It is defined by the following equation :

$$\Theta(t + \vartheta) = \kappa \cdot V(t) + 2\gamma_1 \cdot \psi(t) \cdot C(t)$$

or, simply, it is assumed that the cells have a certain lifespan.

3.2.3 Floating Cyst
Floating cyst population $F(t)$ is assumed to behave as follows :

$$\begin{cases} \frac{\Delta F(t)}{\Delta t} & = \alpha \cdot \psi(t) \cdot V(t) - \gamma_2 \cdot \psi(t) \cdot F(t), \\ F(t) & \geq 0, \end{cases} \quad (4)$$

where $\alpha \cdot \psi(t) \cdot V(t)$ is the number of vegetative cells that turn into floating cysts ; and $\gamma_2 \cdot \psi(t) \cdot F(t)$ is the number of floating cysts that turn into vegetative cells.

3.2.4 Nutrient Function
The nutrient function $K(t)$ satisfies the following dynamics :

$$\begin{cases} \frac{\Delta K(t)}{\Delta t} & = \epsilon - \sigma \cdot V(t), \\ K(t) & \geq 0, \end{cases}$$

where ϵ is the amount of nutrients added at a given time. The above equation basically says that the change in the amount of nutrients in the system is due to a constant supply ϵ coming in minus the amount being consumed by the population.

4. METHODOLOGY
Arrays were used to represent the different lifecycle stages. Each element of the array represented a population level at a given day. Each array were given initial values, and succeeding elements were iteratively derived.

Experiments done for this paper used the following constant values :

$$\begin{array}{ll} \alpha = 0.0, & \kappa = 0.3, \\ \gamma_1 = 1.0, & \gamma_2 = 0.0, \\ \vartheta = 5, & \varsigma = 120, \\ \sigma = 0.005. & \end{array}$$

Other values such as μ, φ, and ω varied depending on the specific experiment being performed. The experiments did not include the effect of the floating cysts in the population. All were implemented in Matlab.

5. EXPERIMENTS
Since bloom initiation and termination in the model is essentially dependent on nutrients, experiments were carried out how on how the level, availability, as well as the periodicity of the nutrients in the environment would affect the resultant bloom. We pegged the following initial values for all the experiments, namely : $V(0) = 0$, $F(0) = 0$, $R(0) = 300$ and $K(0) = 1$.

The first set of experiments were ran with the assumption of an all-year round availability of nutrients. While the nutrient level could drop due to consumption by the phytoplankton, it is linearly(not instantaneously) replenished. Another crucial assumption regarding the setup is the existence of a nutrient *cap*- while the consumed nutrients could be replenished, it could never exceed a certain value, even during the periods without consumption.

Bifurcation plots were produced to determine the stability of population dynamics as a function of sexual reproduction rates and asexual reproduction rates. The maximum levels achieved by the population yearly for 200 years were plotted against sexual reproduction rates and asexual reproduction rates. The more spread the points associated with a certain rate value are, the less stable the population behavior is. Conversely, points that aggregate almost to singular value denote a very stable behavior.

The second set of experiments modeled the presence of nutrients as discrete events : nutrients were only made available during certain periods of the year. In some ways, the setup is inspired by the observation of Azanza et al[11] where they postulated the importance of sediment mixing and turbulence as bloom-initiation events, at least in Manila Bay. This would, in part, explain the importance of seasonal weather in the initiating blooms, since winds are required for such sediment mixing to occur. Nevertheless, it must be pointed out here that the discrete bloom-initiating events in our model are primarily nutrient-based. Likewise, the end of a bloom is also nutrient-related(this time due to the lack of nutrients). Thus, in the current model, bloom-initiation and termination are tied. In contrast, while it is postulated that winds initiate blooms, it is not yet certain that the cessation of the said wind patterns triggered the end of the bloom .

Two aspects of discrete events were explored : duration and intensity.

In the duration experiment, a constant level of nutrient was made available to the system daily, and the effect of the number of days determined.

In the intensity experiment, nutrient was only made available in the system for a single day, but different values
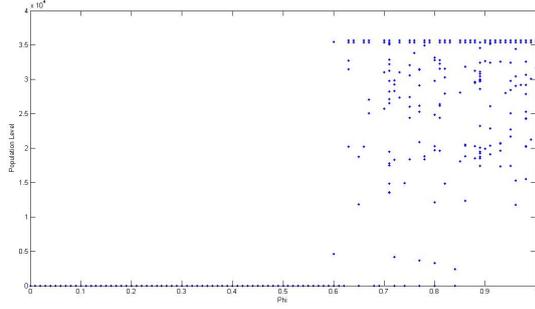
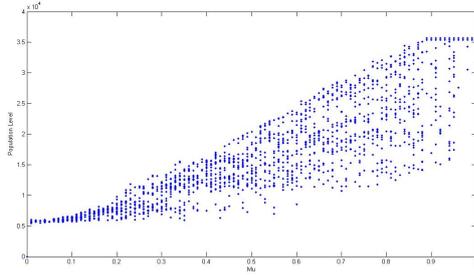**Figure 2: Yearly maximum vegetative cell population for 19 years with $\mu = 1$ (Note : The X-axis are values of φ.)**

Figure 3: Yearly maximum vegetative cell population for 19 years with $\varphi = 1$ (Note : The X-axis are values of μ.)

were tested for different runs. In vivo, it is conceptually equivalent to culturing phytoplankton in a medium initially replete with nutrients but with no replenishment : one such experiment was done in [2].

5.1 Constant Nutrients
5.1.1 Changing Percentage of the Population undergoing Sexual or Asexual Reproduction
The experiments done here looked at the maximum population achieved by the system while varying the values of both μ, the percentage of the population undergoing sexual reproduction, and ϕ, the percentage for those undergoing asexual reproduction. Both μ and ϕ varied from 0 to 1 with a stepsize of .01. The values ϵ and ω were kept constant at 1.5 and 1, respectively.

5.1.2 Changing Number of Offsprings
For this experiment, the number of offsprings produced by a cell at any instance of sexual reproduction was modified, varying from 1 to 20. The population was fed only from days 11 to 50. The amount of nutrients fed is set at an intensity level of 50. μ and φ were set to 1.0.

5.2 Changing Nutrients
To look at the effect of changing nutrients to the population levels and periodicity, two experiments were undertaken. For the first experiment, the population was only fed nutrients on a single day. The system was run multiple times, with each run increasing the amount of nutrients fed. μ and φ were both set to 1.0, and ω at 1. The system was run at 14 days, with the intensity level increasing
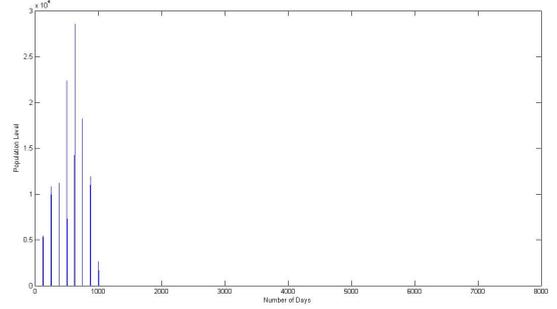

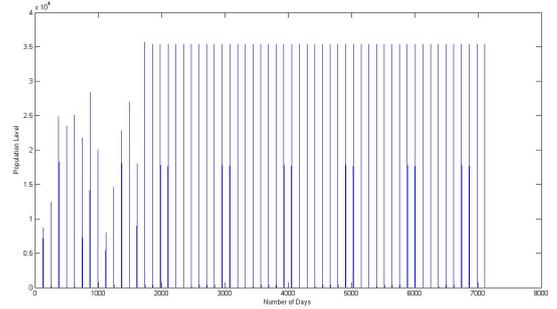**Figure 4: Graph of $V(t)$ at $\varphi = 0.59$, $\mu = 1$.**

Figure 5: Graph of $V(t)$ at $\varphi = 0.93$, $\mu = 1$.

from 1 to 50 and the population was fed at day 3. For the second experiment, the duration of the nutrient feed was swept from 1 day to 10 days. The nutrient feed was started on the 3rd day.

5.2.1 Changing Intensity
For this experiment, the population was only fed nutrients on a single day. The system was run multiple times, with each run increasing the amount of nutrients fed. μ and φ were both set to 1.0, and ω at 1. The system was run at 14 days, with the intensity level increasing from 1 to 50 and the population was fed at day 3.

5.2.2 Changing Durations
For this experiment, the duration of the nutrient feed was swept from 1 day to 10 days. The nutrient feed started on the 3rd day.

6. RESULTS AND DISCUSSION
6.1 Constant Nutrient
6.1.1 Changing Percentage of the Population undergoing Sexual or Asexual Reproduction
The initial experiment performed kept μ constant while φ varied from 0 to 1. A representative bifurcation plot is shown in Figure 2. It can be seen that for a given value of μ, there is a minimum value of φ required for the population to sustain itself. Below such value, the population faces annihilation as shown in Figure 4. As the value of μ is increased, this minimum value of φ decreases. There seems to be no relationship between the maximum attainable population level and φ.

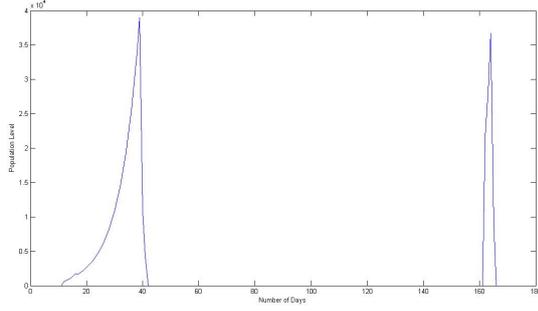It is notable in Figure 2 that there are only few points that aggregate to a single value. The lack of a singular point de-

Figure 6: Graph of $V(t)$ at $\omega = 1$.

Figure 8: Graph of $V(t)$ for $\epsilon = 1$ to 50.
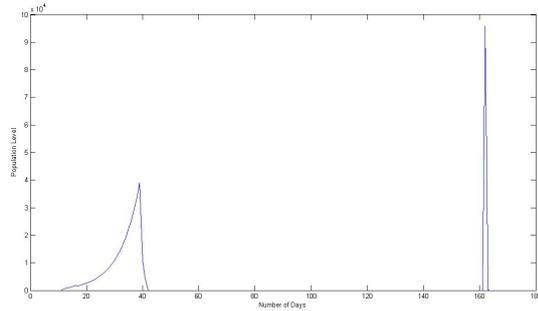

Figure 7: Graph of $V(t)$ at $\omega = 20$.

notes the absence of a perfectly periodic population. However, as shown in Figure 5, sustainable populations need not be periodic. Alternatively, it could be argued that these populations eventually achieve perfect periodicity, albeit after an extended period of time.

Another experiment was run where φ was kept as a constant, and μ was swept from 0.00 to 1.00 at a 0.01 step size. A representative bifurcation plot is shown in Figure 3. As in the previous setup, for a given φ, there is a minimum value for μ required for the population to sustain itself. In general, beyond this minimum value, the maximum attainable population level increases linearly with μ and plateaus before μ reaching 1.00. Like in the previous setup, there were also very few points that aggregated to a single value.

6.1.2   Changing Number of Offsprings
Changing the number of offsprings does not affect the initial bloom, which makes sense because they only depend on the initial number of resting cysts, which is the same for all setups. The effect of changing the number of offsprings can be first seen in the second bloom, where population levels varied across setups. Figure 6 shows a setup with number of offsprings set at 1. It can be seen that the second bloom is significantly lower than the second bloom in Figure 7, which is a setup with the number of offsprings at 20. In general, the higher the number of offsprings, the bigger the subsequent blooms become. However, there is a limit to this increase, where no matter how many offsprings are produced, the size of the subsequent blooms remain the same. This is due to the system being unable to support the large amount of vegetative cells. Thus, not all resting cysts become vegetative cells. Therefore, even if two setups have the same vegetative cell population, the setup with higher number of offsprings will have more res-
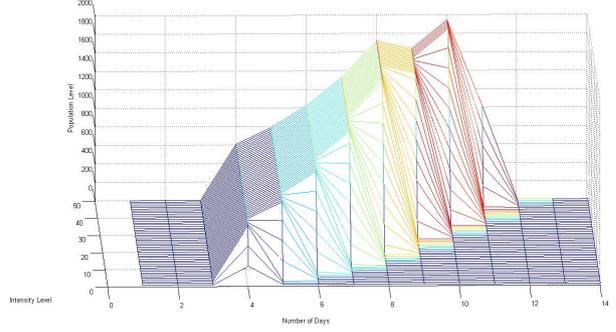
ting cysts. This shows that having a larger number of offsprings can make a population more prone to subsequent blooms via outlier effects, because they have more resting cysts that could potentially become vegetative cells.

6.2   Changing Nutrients

6.2.1   Changing Intensity
The experiment performed on changing the intensity level of the nutrients shows a single bloom whose end varies, depending on the intensity level introduced. Figure 8 shows the result of this experiment. The general trend is that as intensity levels increase, both the duration of the blooms and the maximum attainable population level (bloom peak) increase. However, it is worth noting that the relationship between the intensity level and the bloom duration is not perfectly linear. There are some intensity level ranges that resulted in indentical temporal plots. Another important insight is that the initial population trending is always the same, regardless of the intensity level. Conceptually, this could mean that observing an ongoing bloom (or at least the number of vegetative cells) would give little indication on when the bloom would end.

6.2.2   Changing Durations
In the 3D plot in Figure 9, all primary blooms have the same maximum vegetative cell population level, except for the 1-day nutrient feed duration. Starting from the 4-day nutrient feed duration a plateau in the primary bloom can be observed and by increasing the duration, the plateau lengthens. However, anything beyond the 10-day nutrient feed duration will not have any effect on the primary bloom. A secondary bloom can be observed starting at Day 7 and beyond, and the population level continues to increase.

It is interesting to note that the secondary bloom occurs days after the nutrient feed has stopped. This happens since the vegetative cells encysted (Figure 11) before the nutrient feed has stopped (Figure 12). Therefore, after the 120-day resting period has passed, there were still enough nutrients to produce a second bloom as shown in the nutrient plot in Figure 12.

Generally, lengthening the duration of the nutrient feed increases the maximum attainable population level of the vegetative cells and resting cysts, as shown in Figures 10 and 11. However, any change on the duration of the nutrient feed does not have any effect on the length of the primary and secondary blooms.
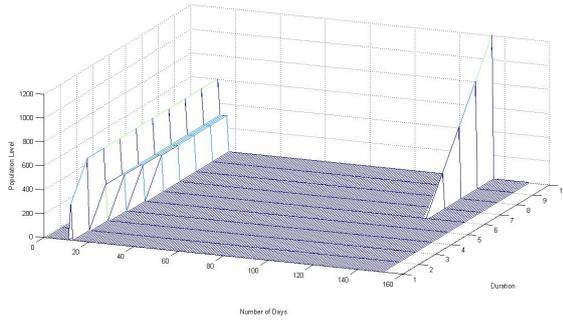
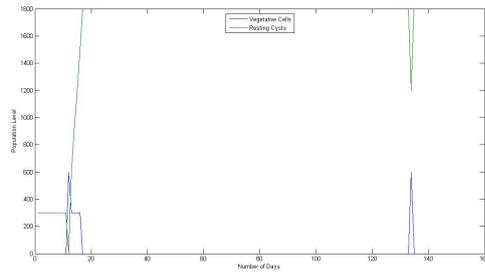**Figure 9: Graph of $V(t)$ for different nutrient feed duration.**

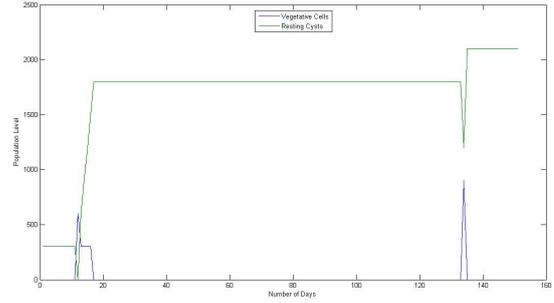**Figure 11: Graph of $V(t)$ at $F(t)$ 9-day feed duration**

Figure 10: Graph of $V(t)$ and $F(t)$ at 8-day feed duration
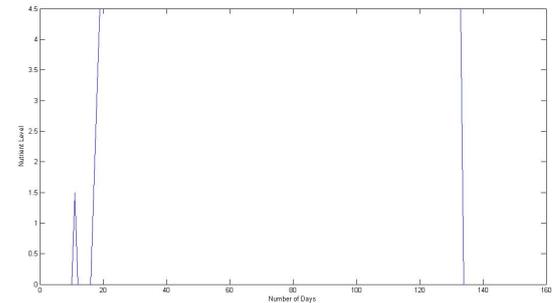

Figure 12: Graph of $K(t)$ at 9-day duration.

7. CONCLUSION AND FUTURE WORKS

7.1 Conclusion

A population-level equational model for the organism *P. bahamense* was presented. It was shown that increasing the number of offsprings will greatly increase the population as long as the nutrient levels will be able to support the population. Also the intensity and duration of the nutrient feed can greatly affect vegetative cell and resting cyst population, and especially for the case of the intensity, the length of the blooms. Finally, the sustainability of a population depends on the percentage of the population allowed to undergo sexual or asexual reproduction at any one time.

7.2 Future works

Future research can incorporate the effects of natural death (spoilage) at various life cycle stages on the length and severity of algal blooms. The "pathway" from vegetative state to floating cysts can also be activated to see what effects it will have on the system. Also, the effects of possible mitigation techniques can also be explored *in silico*. The effect of the phase shift can be studied in future papers. And finally, ABM can be used to further study spatial concerns of algal bloom.

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