Internal dynamics of NPZD type ecosystems models

Group project

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Contents

List of Figures

CHAPTER 1

Introduction

The carbon cycle is the chemical back borne of all life on earth. The amount of carbon present in the earth is constant, but it follows complex relationships where all the earth natural components are present via various chemical, physical, geological, and biological processes.

It is particular important, the role of marine ecosystems in this carbon cycle. The ocean approximately absorbs 2 Pg of CO_2 per year, which is around one third of the emissions produced by the humans. The CO_2 exchange between the atmosphere and the ocean is led by the CO_2 concentration difference between the air and ocean, which indeed is influenced by the CO_2 uptake by the phytoplankton through photosynthesis.
Zooplankton is the primary consumer of phytoplankton, which,in turn, is the primary food source of larval fishes. Finally, the phytoplankton death as well as the zooplankton excretion produces an organic waste called detritus. Whereby a small part is remineralized and comes back to the initial state as nutriment for phytoplankton.

Modelling marine ecosystems is useful to analyze how the carbon cycle is impacted by the ocean [1] but also for studying other natural processes such as the changes in fishing activity due to the atmospheric phenomena [2] or simply the nutrient flow in complex aquatic environments [3] among others.

Given the motivation to study the ocean ecosystem modelling problem from a biological point of view. In this project we aim to implement the NPZD models presented in [4] by means of numerical methods, experiment with the parameters of the models, analyze their dynamics and propose an extension of the original model.

Chapter 2

NPZD model

2.1 Definition and parameters

This project studies the marine ecosystem modelling problem. The publication by Oschlies and Garçon [5] proposes a simple 4 component model with their corresponding mathematical expressions. NPZD type models simulate the concentrations of the following four marine ecosystem components: Dissolved inorganic nitrogen (N), phytoplankton(P), zooplankton(Z) and detritus(D) given in mmol N m^{-3}. See figure 2.1 and 2.2 for a diagram of the dynamics of the system.

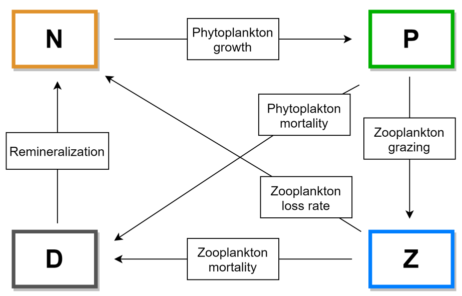

Figure 2.1: Qualitative relationship of a NPZD model

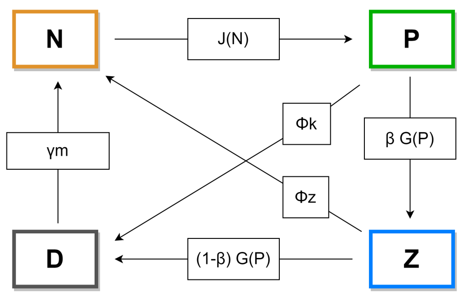

Figure 2.2: Parametric relationship of a NPZD model

The reference publication for this project [4] proposes three similar models. The difference between the three models presented in the following are in these ODE systems, in particular in the loss terms of zooplankton and phytoplankton. While the first model, model LLM, assumes a linear mortality of both, phytoplankton and zooplankton, the second model, model LQM, contains an additional, quadratic loss term of zooplankton. The third model, model QQM, finally considers linear and quadratic mortalities of both variables.

This three models can be expressed in terms of 4 nonlinear ordinary differential equations that contains contains the concentrations of the marine ecosystem components aforementioned (N,P,Z,D).The dynamics of the three models are the following:

- LLM and LQM:

$$
\begin{aligned}
\frac{\partial N}{\partial t} &= -J(N,I)P + \Phi_Z Z + \gamma_m D,\\
\frac{\partial P}{\partial t} &= (J(N,I) - \Phi_P)P - G(\epsilon, g, P)Z,\\
\frac{\partial Z}{\partial t} &= (\beta G(\epsilon, g, P) - \Phi_Z - \Phi_Z^*)Z,\\
\frac{\partial D}{\partial t} &= \Phi_P P + ((1-\beta)G(\epsilon, g, P) + \Phi_Z^*)Z - \gamma_m D
\end{aligned}
$$

- QQM:

$$
\begin{aligned}
\frac{\partial N}{\partial t} &= (-J(N,I) + \Phi_P)P + \Phi_Z Z + \gamma_m D,\\
\frac{\partial P}{\partial t} &= (J(N,I) - \Phi_P - \Phi_P^* P)P - G(\epsilon, g, P)Z,\\
\frac{\partial Z}{\partial t} &= (\beta G(\epsilon, g, P) - \Phi_Z - \Phi_Z^*)Z,\\
\frac{\partial D}{\partial t} &= \Phi_P^* P^2 + ((1-\beta)G(\epsilon, g, P) + \Phi_Z^*)Z - \gamma_m D
\end{aligned}
$$

As can be appreciated, the three models are very similar except for the quadratic loss terms of the phytoplankton and zooplankton. This terms are of great importance for NPZD because they model either the flux from phytoplankton to detritus (LLM and LQM) or the flux from phytoplankton and zooplankton to detritus (QQM).This can be summarised as follows:

- LLM model assumes a linear loss of both, phytoplankton and zooplankton.
- LQM model assumes a linear loss of phytoplankton but a quadratic loss of zooplankton.
- QQM model assumes a quadratic loss of both, phytoplankton and zooplankton.

Therefore, it is possible convert the LQM model to LLM by setting the Φ_Z^* parameter to zero.

The modelling of the phytoplankton growth follows this expression:

$$J(N,I) = \mu_m \cdot f_N(N) \cdot f_I(I) \tag{2.1}$$

with :

$$f_N = \frac{N}{k_N + N}; f_I(I) = \frac{I}{k_I + I} \tag{2.2}$$

f_N and f_I are terms representing the current nutrients and light available. These are modeled to grow very fast until reach the half of their maximum capacity, and slowing down the growth once achieved (more information in section 3.1).

Regarding to the zooplankton grazing the equation, the [4] publication proposes the following equation:

$$G(\epsilon, g, P) = \frac{g\epsilon P^2}{g + \epsilon P^2} \tag{2.3}$$

$G(\epsilon, g, P)$ is a Holling type III function that aims to recreate the saturation behaviour of the zooplankton grazing.

2.2 Equilibrium points

In [4] the equilibrium points are evaluated analytically. These are very useful from a mathematical point of view as well as biological in order to evaluate which parameters affect the dynamics of the system as well as their stability. The results were the following:

- **LLM**:
  - $E^*_{LLM_1} = (N^*_1(S), 0, 0, 0)$
  - $E^*_{LLM_2} = (\frac{k\Phi_P}{\mu_m - \Phi_P}, P^*_2(S, u), 0, \frac{\phi_P}{\gamma_m} P^*_2(S, u))$
  - $E^*_{LLM_3} = (N^*_3(S, U), P^*_3(S, U), Z^*_3(S, U), D^*_3(S, U))$
- **LQM**:
  - $E^*_{LQM_1} := E^*_{LLM_1}$
  - $E^*_{LQM_2} = (E^*_{LLM_2})$
  - $E^*_{LQM_3} = (N^*_3(S, U), P^*_3(S, U), Z^*_3(S, U), D^*_3(S, U))$
- **LQM**:
  - $E^*_{QQM_1} := E^*_{LLM_1}$
  - $E^*_{QQM_2} = (N^*_2(S, U), P^*_2(S, U), 0, \frac{\Phi^*_P}{\gamma_m} P^*_2(S, U)^2)$
  - $E^*_{QQM_3} = (N^*_3(S, U), P^*_3(S, U), Z^*_3(S, U), D^*_3(S, U))$

Regarding to the LLM model there are three equilibrium points/situations. The first one represents the situation in which because of either the lack of insolation or low initial nutrient condition, the phytoplankton does not reach a sufficient

concentration to growth and therefore the zooplankton neither.So, because it is a mass conserving system, which means that the sum of all the right terms in equations are zero (neither enters nor leaves mass), consequently there are only free nutrients (N) in the water with the same concentration than the original sum of each initial concentration :$S = \sum N_0 + P_0 + Z_0 + D_0$
The second one represents the situation whereby coexists in equilibrium N,P and D. The nutrients depends on the phytoplankton loss as well as the remineralization rate. P is a state that relies on the parameters and the initial sum of concentrations and D is proportional to P by the relation of phytoplankton loss and remineralization rate. The last one represent the situation where exists a coexistence among the 4 variables, that depends on the parameters.

Related to the LQM model, it has the same equilibrium points if it is followed the assumption of $Z^* = 0$ which has sense due to the mass conserving system.

Finally the QQM model has a very similar equilibrium points in shape in compairson with the LQM but it differs their values due to the addition of the zooplankton loss quadratic term.

2.3 Implementation details

Although the finality of the report is not to go into technical details of the simulations, we consider interesting to provide a brief explanation of the techniques used in the project.
We have to integrate a system of non-linear differential equations, which returns the concentration value of the model nutrients in a specific time period according to the formulations section 2.1. Due to the impossibility of solving this equations analytically it becomes necessary the implementation of numerical methods to solve them. By the aid of Python's scientific computing packages, we have implemented a basic iterative method to solve differential equations, Euler's method:

$$y_n = y_{n-1} + \Delta t \cdot y'(x_{n-1}, y_{n-1}) \tag{2.4}$$

It computes the value of the element in time t with the aid of the derivative value of the element at the previous moment. However, this approach has a slow convergence and it's performance highly relies on the timestep Δt. We also implemented the ODE integrator provided by the python module Scipy [6], it implements advanced numerical methods for integrating ODEs (Runge-Kutta method).

2.4 Model simulations

Once explained the model and the numerical method to solve its differential equations it were obtained the next results:

With S varying until 200 (high concentration), the nutrients grow almost linearly, and the other components increase very slowly,until they reach somewhere in the region of 170 $molNm^{-3}$, where detritus and phytoplankton grow suddenly.

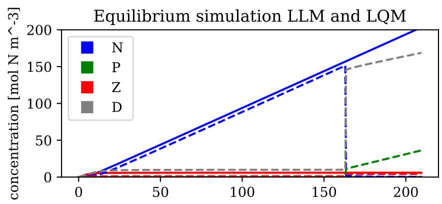

Figure 2.3: Equilibrium of LLM-LQM model (S varies until 200)

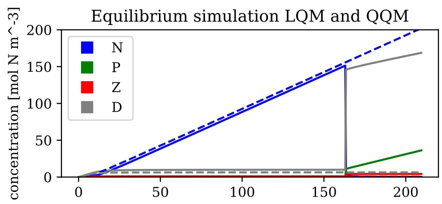

Figure 2.4: Equilibrium of LQM-QQM model (S varies until 200)

In the region until 30 $molNm^{-3}$, the LLM model estimates a growth in nutrients and zooplankton whereas QQM model and LQM model simulates a situation where the detritus increases considerably.

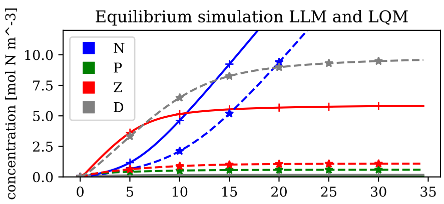

Figure 2.5: Equilibrium of LLM-LQM model (S varies until 35)

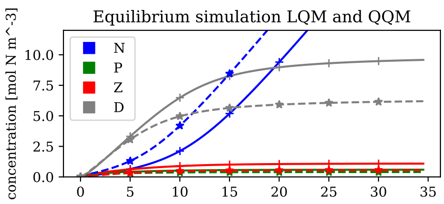

Figure 2.6: Equilibrium of LQM-QQM model (S varies until 35)

When the concentration is small, the behaviour of the model is more linear in comparison with the previous one,phytoplankton turns into the predominant component.

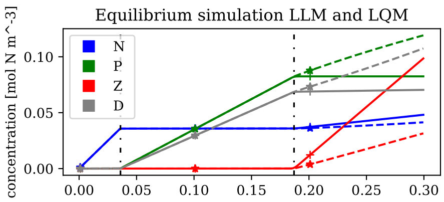

Figure 2.7: Equilibrium of LLM-QQM model (S varies until 0.3)

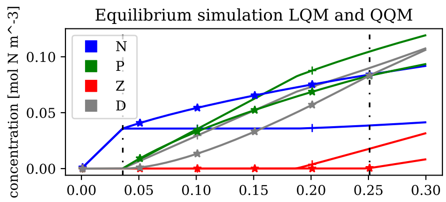

Figure 2.8: Equilibrium of LLM-LQM model (S varies until 0.3)

Subsequently, it was simulated the first situation of equilibria, in which all the mass becomes as a nutrient in the marine ecosystem.

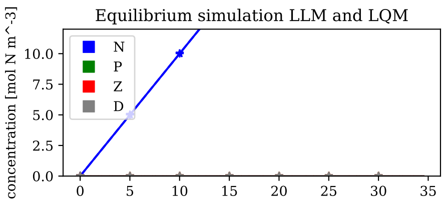

Figure 2.9: First Equilibrium point LLM-LQM

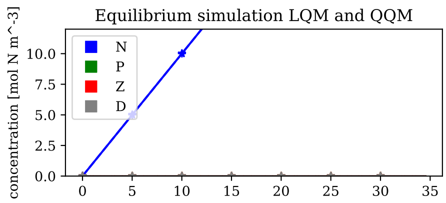

Figure 2.10: First equilibrium point LQM-QQM

Finally, it was simulated a temporal phase diagram with the objective of observing the evolution of each component of LQM model as well as LLM model. As it can be seen, the linear model simulates an environment in which the zooplankton grows very fast, while in the LQM model the detritus grows faster than in LLM. This is because of the addition of the zooplankton quadratic loss in the model.

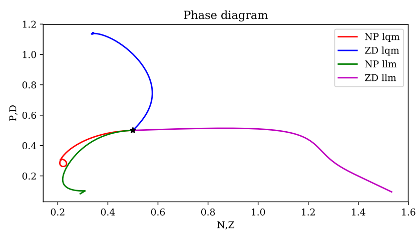

Figure 2.11: Plot of the temporal evolution of NPZD components. Y axis represents the P and D and X axis contains N and Z

Chapter 3

Light intensity modelling

3.1 Motivation to model light

Phytoplankton obtains energy through the process of photosynthesis and must therefore live in the well-lit surface layer (known as the euphotic zone) of an ocean, sea, lake or other body of water. Phytoplankton accounts for about half of all photosynthetic activity on Earth [1] [2] And phytoplankton is on the base of the food chain in marine ecosystems, they are the basis for the vast majority of oceanic and freshwater food webs.

The light intensity (I) is a key player in the phytoplankton ecology. During photosynthesis, they assimilate carbon dioxide and release oxygen. If solar radiation is too high, phytoplankton may fall victim to photodegradation. If too low, it is an impediment for reproduction. For growth, phytoplankton cells depend on nutrients, which enter the ocean by rivers, continental weather and glacial ice meltwater in the poles.

As explained in the previous sections the proposed NPZD model takes a rather simplistic approach to model the relationships between the four resources. Let's analyze the partial derivative of phytoplankton ($\partial P/\partial t$), equation 1. The only growth term is $J(N, I) \cdot P$ and all the other parameters (death rates and grazing rate) are negative terms that represent a decrease in the phytoplankton.

$$\frac{\partial P}{\partial t} = (J(N, I) - \Phi_P)P - G(\epsilon, g, P)Z$$

In the model, the growth of phytoplankton is dependent on the light (I), and the amount of nutrients (N) available. Function J is composed of two monotonously increasing functions f_N and f_I that are formulated according to Michaelis-Menten. These functions describe the present light and nutrient conditions separately. A maximum growth rate μ_m is weighted by one or more saturation terms.

$$J(N, I) = \mu_m \cdot f_N(N) \cdot f_I(I) \qquad f_N = \frac{N}{k_N + N} \qquad f_I(I) = \frac{I}{k_I + I}$$

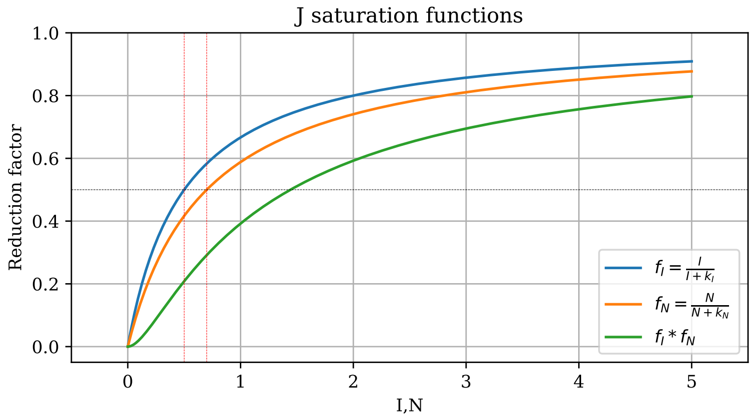

Figure 3.1: Plot of the saturation functions with k_N=0.7 and k_I=0.5

The parameter I (light intensity) is taken as a static parameter. We think that this is a plain approach and there is room for studying a more complex modelling of this parameter.

3.2 Proposed approaches

We present two approaches to model the light intensity parameter (I) based on some assumptions. Disclaimer: we are not biologists and we do not know if this assumptions make sense in real world settings.

3.2.1 Attenuation factor based on S parameter

We model the intensity of light based on the quantity of particles that there is in the water. If we sum the four parameters (N,P,Z,D) we get the total concentration of particles in the water ($mmolNm^-3$), parameter S. We assume that a quantity of light gets reflected/absorbed by the particles in suspension in the water, so the final light impacting the phytoplankton is lower.

$$S = N + P + Z + D$$

We propose to use a constant times an inverted logarithm base 10 shifted by 10 units in the x axis. So when S=0 the function gives the max value (the constant) and the higher the S the smaller the value. There is parameter n which gives the velocity of attenuation see figure X for a representation of the function for various values of n.

$$f_S = log_{10}(S + 10)^{-n}$$

The second proposal is to use a ponderation value for each parameter. It makes

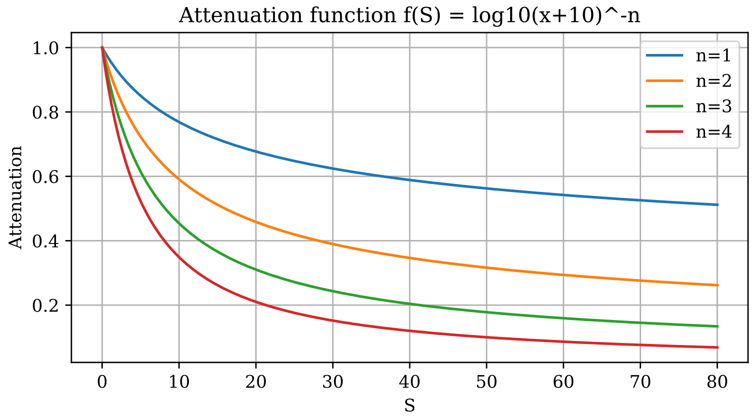

Figure 3.2: Attenuation functions with various n values

sense for each component to have different light attenuations. So by taking the same function as for the simple case and using a different value of n for each component we can get an averaged value of the light attenuation.

$$f_S = \frac{N}{S} * f_N + \frac{P}{S} * f_P + \frac{Z}{S} * f_Z + \frac{D}{S} * f_D \qquad f_X = log_{10}(S + 10)^{-n_X}$$

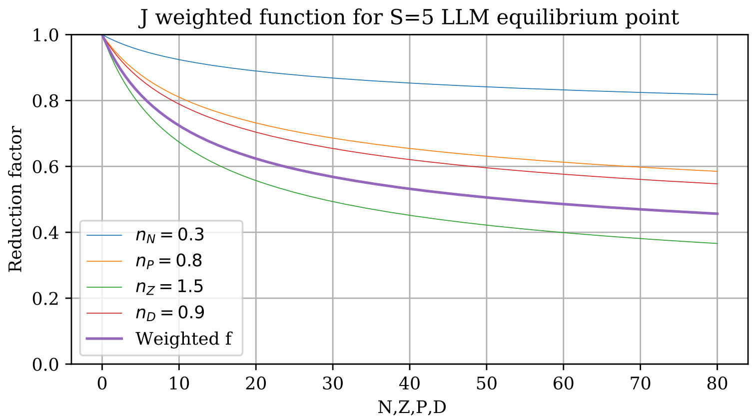

Figure 3.3: Weighted attenuation functions with various n values

3.2.2 Temporal modelling of light intensity (daily/seasonal)

In this case we model the intensity of the light based on the periodic changes of it. The light intensity varies by the earth rotation (day and night cycle) and by earth revolution (season cycle). We propose simple sinusoidal functions to model the periodic relationship. For the daily variation we add an extra parameter s to represent the shift between peak sunlight hour and midday. See figure 3.4.

$$f(t) = \frac{1}{2}(1 - cos((t - s/24) \cdot 2\pi))$$

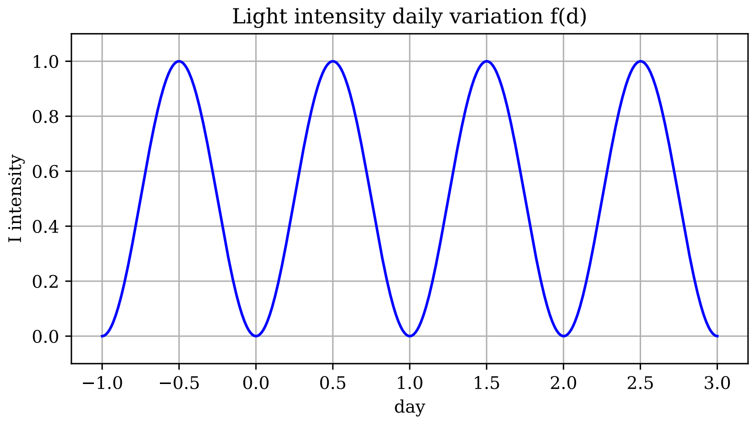

Figure 3.4: Daily light variation function plot with $s = 0$

For the yearly variation we have two parameters, the first is the s parameter, to represent the shift in days between beginning of the year and the winter solstice (9 days) and the second is the μ_{max} which represents the max variation (relative) between the average and the max/minimum light due to seasonality. This last parameter should be tuned depending on the latitude we are conducting the experiment, if we are close to equator this parameter will be close to 0 (as there is little variation in the light) and if close to the poles then the value will be larger. See figure 3.5.

$$f(y) = 1 - \mu_{max} \cdot cos((y - s/360) \cdot \frac{2\pi}{360})$$

3.3 Results with proposed approaches

In this section we show the results we obtained using numerical methods (see section 3.3 for details) and show an intuition of the results it would have in the real world.

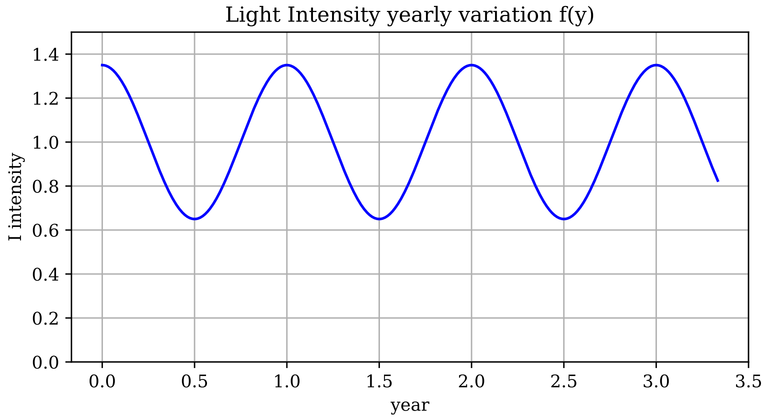

Figure 3.5: Seasonal light variation function plot with $s = 0$ and $\mu_{max} = 0.35$

3.3.1 Attenuation function based on S parameter

The light attenuation due to particles in suspension (N parameter) is analyzed in this section. We use numerical methods to compute the behaviour of the model. This modelling of the light affects the three models in a similar fashion, it reduces the growth function $J(N, I)$ so the phytoplankton quantity will be lower, the zooplankton and detritus quantity (that are directly proportional to P) will also be lower and Nutrients(P) will be higher as the only negative term in the $\partial N/\partial t$ is $J(N, I)$. See figures 3.6, 3.7, 3.8 for representations of the equilibrium points on the different models with the n parameter equal to 0.8.

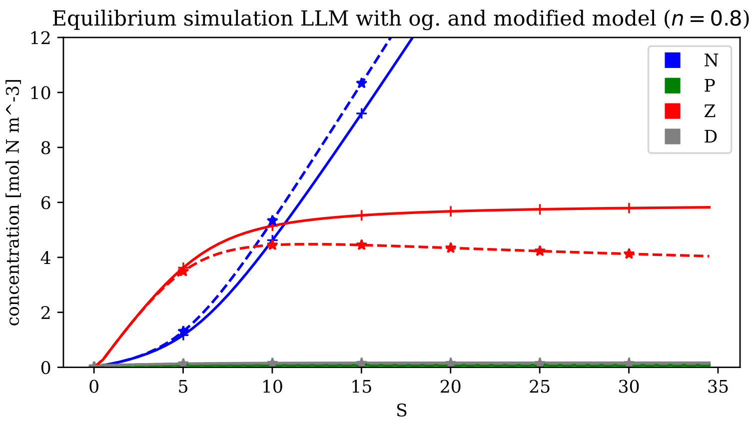

Figure 3.6: Equilibrium points of the models per S value. LLM original model in solid line and LLM with light intensity with dashed line (n=0.8).

Further experiments should be done to see if the light attenuation caused by particles in suspension is real and has an impact in real ecosystems. Our intuition is that in shallow water ecosystems this modelling would not have any impact as the quantity of water is low, but in deeper ecosystems with already a low quantity of light this modelling would be good addition.

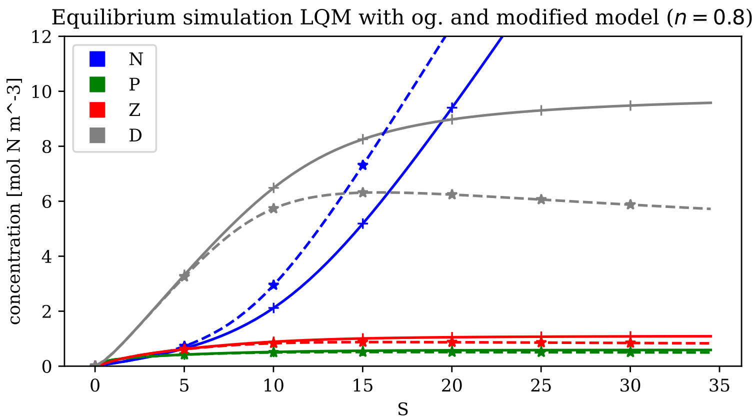

Figure 3.7: Equilibrium points of the models per S value. LQM original model in solid line and LQM with light intensity with dashed line (n=0.8).

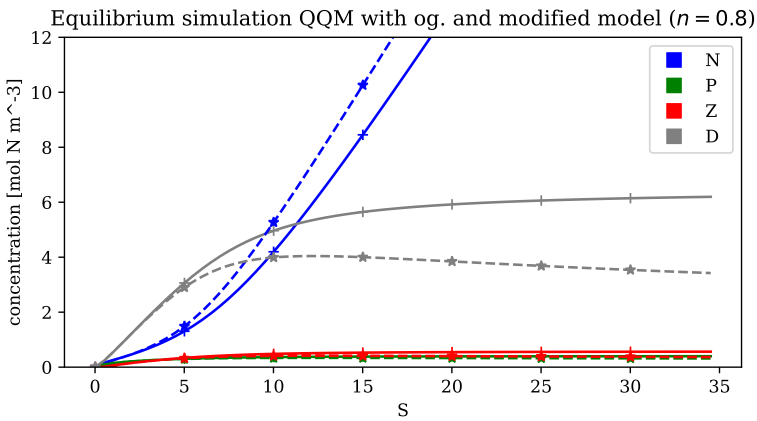

Figure 3.8: Equilibrium points of the models per S value. QQM original model in solid line and QQM with light intensity with dashed line (n=0.8).

3.3.2 Seasonal modelling of I

In the original model they assume a constant light factor (I). This makes sense if we are modelling a region close to equator, but it might be inaccurate if we are working on a region closer to the poles. Because of the earth translation there is a difference in the quantity of solar energy that irradiates the earth. We model this with a simple sinusoidal function.

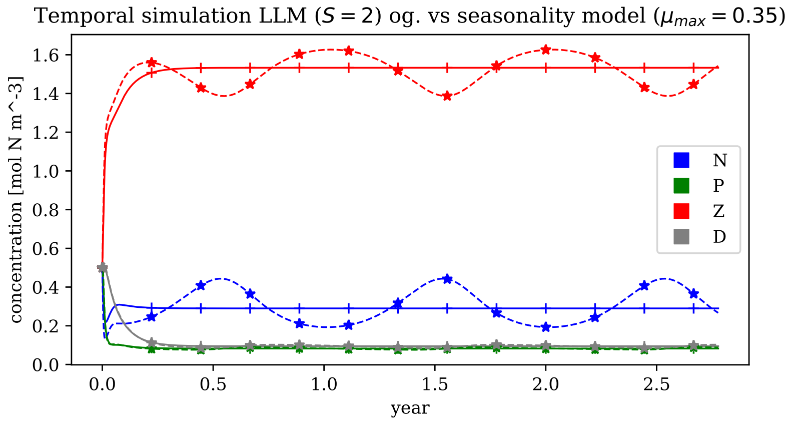

Figure 3.9: Temporal simulation of LLM model. LLM original model with solid line and LLM with light intensity with dashed line (μ_{max}=0.35).

In this case studying the equilibrium doesn't make much sense as it will not get to a fixed equilibrium point (trigonometric functions do not have a zero derivative). So instead we have done some temporal simulations to see the impact of the season in the proportion of nutrients. We also did some experiments with the daily light variation but we discarded them as it did not make much sense to apply such 'fast' changes when this model is quite 'slow', the time horizon is year/multi year simulations instead of shorter term objectives.

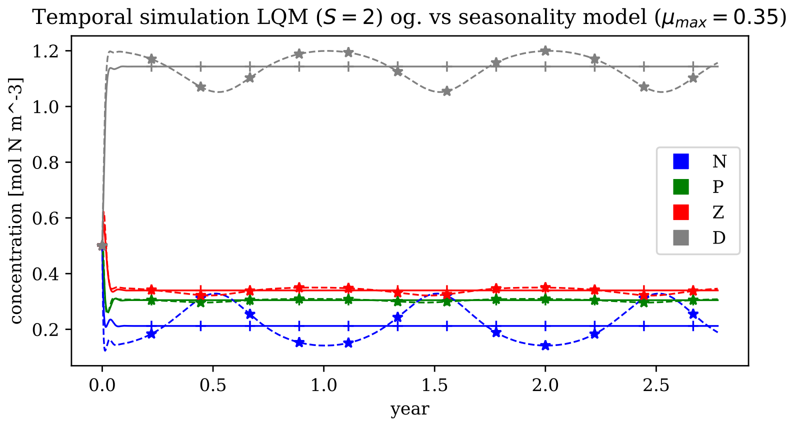

Figure 3.10: Temporal simulation of LQM model. LQM original model with solid line and LQM with light intensity with dashed line (μ_{max}=0.35).

See figures 3.9, 3.10, 3.11 for temporal simulations of the different models using a seasonal modelling of I. And figure 3.12 for a comparison of the LLM model with two different n values.

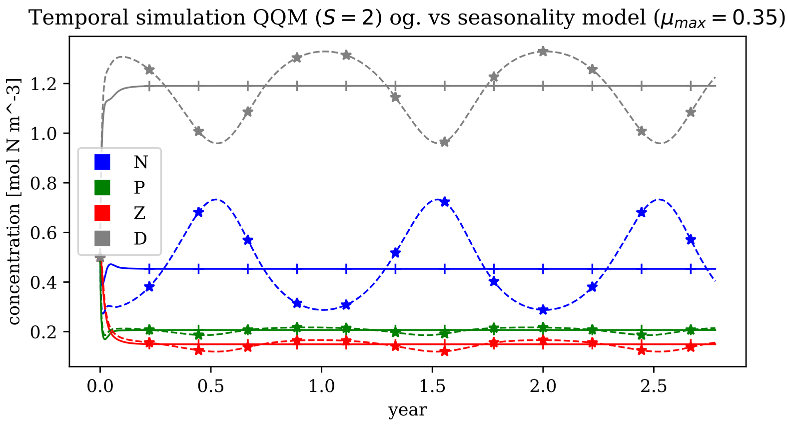

Figure 3.11: Temporal simulation of QQM model. QQM original model with solid line and QQM with light intensity with dashed line (μ_{max}=0.35).

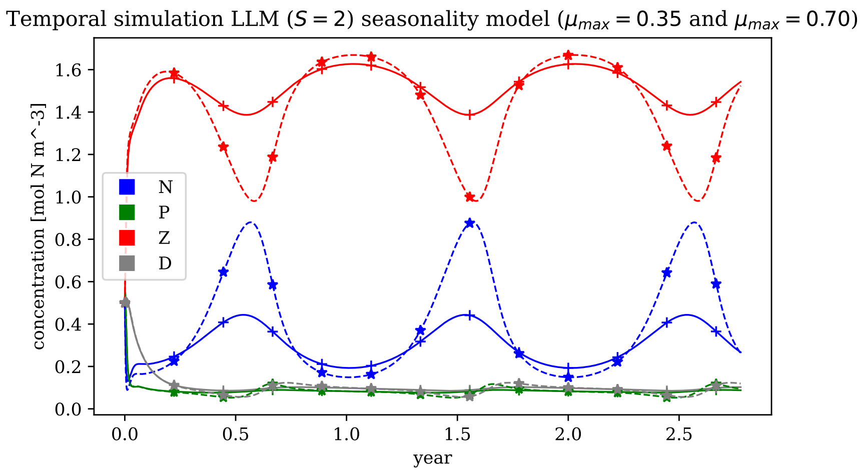

Figure 3.12: Temporal simulation of LQM model with μ_{max}=0.35 (solid line) and μ_{max}=0.75 (dashed line)

In figure 3.12, it is interesting is the behaviour of a larger μ_{max} has on the simulation. It produces a biased movement of the N and Z components, where instead of following and ondulating fashion it produces some 'peaks'. In the nutrients it produces higher max concentration values but the minimum concentration values remain similar if not the same. The inverse behaviour occurs on the Zooplankton.

Chapter 4

Conclusions

In the first part of the course we have learnt the basics concepts of dynamical systems theory and how to apply them to biology problems. We have seen from first hand how mathematics and learning the theory first, gives us a powerful framework to approach applied problems, in this case biology problems. Although we are not experts (nor knowledgeable) in the topic we have been able to understand the biological aspects and how they relate to math; it has been a delightful experience to manage to do all of this in such a short time-frame. This project is the culmination of this part of the course.

In this project we have studied and extended a scientific publication in the field of ecological modelling. Knowing the basic dynamics of the model, depicted by its equilibrium solutions, it is possible to determine the model's behaviour under specific conditions. Besides doing a qualitative analysis of the behaviour of the model we have implemented numerical simulations (of it) to study specific cases and get a feeling on how the theory marries with reality.

Our proposal for the novel part of the project is to do a more complex modelling of the light intensity, in the original model it was modelled as a constant. We propose two approaches, one is to model a relationship of the light intensity with the quantity of particles in the water, and the second is to model the light according to the earth rotation/translation, basically the day/night cycle and the seasonal cycle. We have suggested models for each proposal, implemented them and analyzed the results of the simulation. We are aware that we have taken a rather applied approach, this may be a bias coming from background (engineering), but anyway it has given us a full understanding of the proposal and how it works.

In our opinion we have done the first part of the job. But we are missing a second part, which is to take a biological approach to the problem. To see if our proposal make sense (from biology point of view), to improve it with the expert knowledge from ecologists and biologists, to contrast the results of the model with real world datasets and to optimize the parameters for specific cases.

Apart from the presented proposals we had many ideas in our discussion sessions, although we ended up discarding them for the present project they are good proposals and could be object of study in future endeavours. I will comment on two of them. The first is to create a spatial model of the NPZD components, given that the biological conditions (sunlight, pressure, oxygen, etc.) vary a lot by different depths, we could propose to study the flows of components from one layer to another of the model, i.e. phytoplankton moving from the top layers to zooplankton in the mid ones to detritus in the last layers. The second is to study genetic algorithms for parameter optimization, this idea came from trying to fit the model to an existing dataset, we studied the different methods and we found that genetic algorithm fitted the problem really well and interested both of us.

We understand the time constraints for this project and we can't aim to produce a full scientific publication in the span of two weeks. Nonetheless this work has been enjoyable, we have learnt a lot about the class concepts and we are eager to work in the future in similar projects!

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