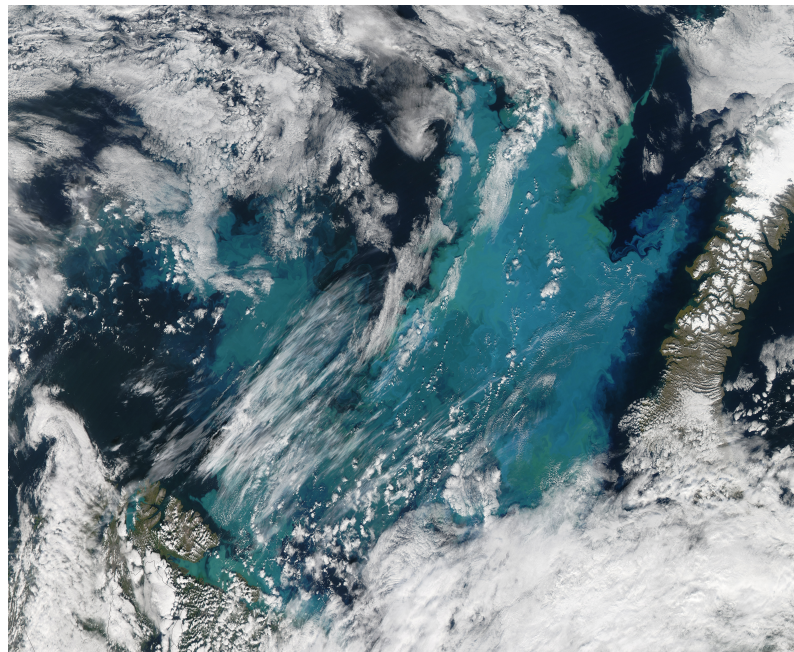


Competition between multiple phytoplankton species in the ocean under various light conditions

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Phytoplankton bloom in the Barents Sea in late August. On the right the Russian island of Novaya Zemlya. Source: <http://earthobservatory.nasa.gov/IOTD/view.php?id=79260>.

Abstract

Phytoplankton, organic cells in bodies of water, can grow rapidly when sufficient light (largest near the surface) and nutrients (largest near the bottom) are available. A numerical model is used to gain insight into the competition of three phytoplankton species in the seasonal and daily light variations of different latitudes. The focus of this study lies on the effects of day-night varying light conditions on top of a seasonal light variability, compared to solely seasonal light conditions. Results show that three species can all survive in an environment without day-night variation, no matter the latitude. But when daily variation is taken into account on top of the already existing seasonal variation, only one species will prevail.

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1 Introduction

Tropical rain forests are often referred to as the green lungs of the earth, as they provide oxygen and consume CO_2 . But next to those forests there is another, more hidden biological organism, which is just as capable of filtering carbon out of the atmosphere and using sunlight to produce biomass, *phytoplankton* (Fig. 1). It accounts for almost half of the global carbon cycle. According to *Field et al.* [1998], Global NPP (Net Primary Production of organic material) is $104.9 \text{ Pg of C year}^{-1}$ ($104.9 \times 10^{15} \text{ g of C year}^{-1}$), with 46.2% contributed by the oceans and 53.8% contributed by the land. Phytoplankton grows in the euphotic zone of the oceans, estuaries and lakes, when there is enough sunlight to support photosynthesis and where there are enough nutrients dissolved. They can grow up to 100 meter deep in the ocean, producing so called Deep Chlorophyll Maxima (DCM's) every summer.

When conditions are optimal, phytoplankton can grow rapidly in a matter of days, producing a so called phytoplankton bloom (see figure on front page). These blooms can often easily be observed from space because of the green color that is produced by the chlorophyll inside the plankton cells. Almost all phytoplankton species are unable to move by themselves (not surprising considering that *phyto* means 'plant' and *plankton* means 'wanderer'), they are subject to the currents of the water. As mentioned earlier, phytoplankton have a significant impact on the global CO_2 budget. But apart from that they could also potentially be harvested for biofuel production [*Scott et al.*, 2003] and they play an important role in the functioning of marine ecosystems, as they are a major food source for fish [*Falkowski*, 2012]. These properties make them an important subject for studies nowadays.

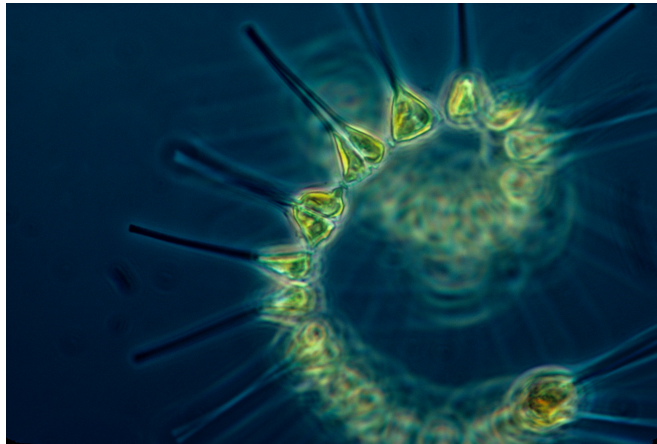


Figure 1: A microscopic view of phytoplankton. The green chlorophyll in its plant cells is clearly visible. Source: <http://www.photolib.noaa.gov/bigs/fish1880.jpg>.

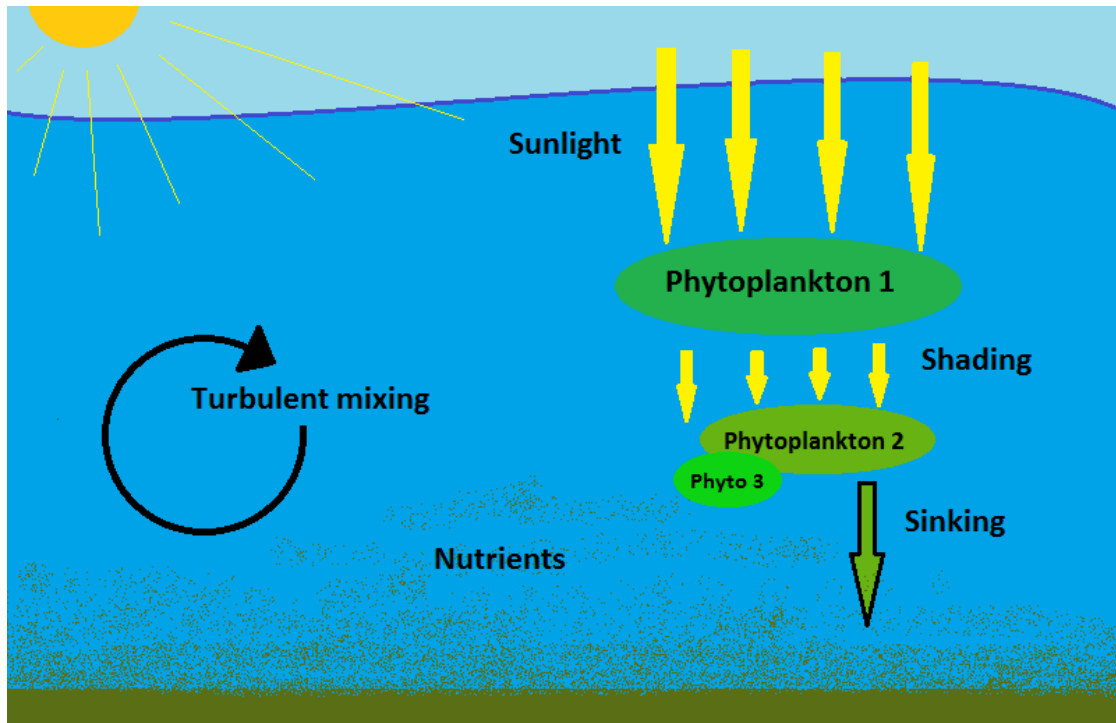


Figure 2: A schematic overview of phytoplankton dynamics.

1.1 Problem

When modelling DCM's for multiple species a problem arises, because the growth characteristics of one phytoplankton species are already very complex as they depend on many different variables. The schematic in Fig. 2 shows an overview of a basic phytoplankton system. The phytoplankton resides in a body of water where light is supplied from above and nutrients well up from the bottom by turbulent mixing. When there is enough of those two resources available they grow, and when the plankton die they sink to the bottom where they are partially recycled into nutrients. Plankton also causes shading of the water column below reducing light for other species that might grow there.

1.2 Research question

On the subject of phytoplankton a lot of work has been done already. Complex numerical models, such as FVCOM¹, have been used to describe phytoplankton [*Luo et al.*, 2012], revealing many details but being computationally very demanding.

More simple models offer less detail, but since they are computationally less demanding, they are very suitable for sensitivity studies as they can look at long term behavior.

Huisman et al. [2006] uses such a 'simple' model and focusses on the growth behavior of phytoplankton at different turbulent diffusivities, at a constant latitude, and with either constant light conditions or seasonally varying light conditions. Aspects that he does not address are e.g. daily variation in light conditions and varying light intensity at different latitudes. Leading to the two main research questions of this thesis:

- How does competition between 3 phytoplankton species depend on seasonal variation in light at different latitudes?
- What happens to phytoplankton competition when daily variation is added to a seasonal light environment at different latitudes?

The way to address these problems is to take a numerical model which uses the same basis as the schematic of Fig. 2 and extend it to three phytoplankton species. And implement a formula to adjust the light intensity, in such a way that it describes incident light at different latitudes and having it account for daily variation. The next section discusses the basic equations which govern such a system. The challenge will be to extend the numerical model that uses these equations to govern more parameters making it a more detailed model but giving insight to the problem. After that the results will be shown in section 3, followed by a discussion in section 4 and conclusions in the last section.

¹The Unstructured Grid Finite Volume Coastal Ocean Model is a prognostic, unstructured-grid, finite-volume, free-surface, 3-D primitive equation coastal ocean circulation model developed by UMASSD-WHOI joint efforts.

2 Materials and Methods

2.1 Theory of the one species model

The plankton model that is used, is based on the following theoretical concepts. It considers a vertical water column in the ocean of depth D and a vertical z coordinate. Here, $z = 0$ is the water surface, and $z = B$ is the bottom of the water column. In this water column there is a phytoplankton population of a certain density (number of cells m^{-3}) and nutrients of a certain density (mmol nutrients m^{-3}) those values are calculated by using reaction-advection-diffusion equations [Huisman *et al.*, 2006].

2.1.1 Phytoplankton and nutrients

Two equations describe the dynamics of phytoplankton and nutrients, respectively:

$$\frac{\partial P}{\partial t} = \mu(N, I)P - mP - v\frac{\partial P}{\partial z} + \kappa\frac{\partial^2 P}{\partial z^2}, \quad (1)$$

$$\frac{\partial N}{\partial t} = -\alpha\mu(N, I)P + \varepsilon\alpha mP + \kappa\frac{\partial^2 N}{\partial z^2}. \quad (2)$$

Here, P is the phytoplankton population, $\mu(N, I)$ is the specific growth rate of the phytoplankton. Furthermore, m is the specific loss rate (or mortality) of the phytoplankton, v is their sinking velocity and κ (here assumed constant) is the vertical turbulent diffusivity, which makes the nutrients mix through the water column. Finally, α is the nutrient content of the dead phytoplankton and ε is the proportion of those nutrients that is actually recycled.

The growth rate $\mu(N, I)P$ of phytoplankton is a function of both nutrients and light, limited by the source that is the least available. This process happens following the Von Liebig's law of the minimum:

$$\mu(N, I) = \mu_{max} \min\left(\frac{N}{H_N + N}, \frac{I}{H_I + I}\right), \quad (3)$$

here, μ is the maximum specific growth rate, H_N and H_I are half-saturation constants for respectively nutrients and light limited growth and \min is the minimum function.

As visible in Fig. 3, higher values of H_N or H_I cause the growth rate to decrease. When a species has a high value of H_N , it is more constrained by nutrients and therefore a better light competitor. When a species has a high value of H_I , the light will be the limiting factor, making it a better competitor for nutrients.

2.1.2 Light

Light is absorbed by turbidity of phytoplankton, water itself or other dissolved substances like the nutrients. To account for this, the model uses an exponential dependence on depth to describe the light intensity at a certain depth, this according to the Lambert-Beer law:

$$I = I_{in} \exp(-K_{bg}z - k \int_0^z P(t, \sigma) d\sigma). \quad (4)$$

In this expression, I_{in} is the incident light intensity, K_{bg} is the background turbidity of the water, k is the absorption coefficient of the phytoplankton and σ is an integration variable accounting for the non-uniform phytoplankton population density².

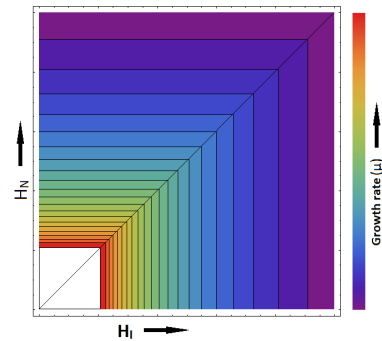


Figure 3: Contour plot of the growth rate dependence on H_I and H_N .

²Huisman *et al.* [2006] Supplementary Information.

2.1.3 Initial boundary conditions

We also need to specify boundary conditions. The model uses the zero-flux boundary condition for the phytoplankton, making sure they do not exist beyond the bottom and top of the water column:

$$\left(-vP + \kappa \frac{\partial P}{\partial z}\right) \Big|_{z=0,B} = 0. \quad (5)$$

Furthermore the zero-flux boundary condition is also implemented for nutrients at the surface while nutrients are steadily supplied from the bottom (with a constant value N_B) by vertical turbulent diffusion. This yields

$$\left(\kappa \frac{\partial N}{\partial z}\right) \Big|_{z=0} = 0 \quad (6)$$

and

$$N_{z=B} = N_B. \quad (7)$$

2.2 Extension to a three species competitive model

The theory of a single plankton species in a water column can be straightforwardly extended to that for multiple species. It is useful to realize that the things that couple the different species of plankton together are the amount of available nutrients and the shading of light by phytoplankton biomass.

Consider again with the formulas for the nutrient and phytoplankton dynamics, but now with two additional species. This yields the equations

$$\frac{\partial P_i}{\partial t} = \mu_i(N, I)P_i - m_iP_i - v_i \frac{\partial P_i}{\partial z} + \kappa \frac{\partial^2 P_i}{\partial z^2} \quad i = 1, 2, 3 \quad (8)$$

and

$$\frac{\partial N}{\partial t} = - \sum_{i=1}^3 \alpha_i \mu_i(N, I)P_i + \sum_{i=1}^3 \varepsilon_i \alpha_i m_i P_i + \kappa \frac{\partial^2 N}{\partial z^2}. \quad (9)$$

The vertical light gradient is now given by

$$I = I_{in} \exp\left(-K_{bg}z - \sum_{i=1}^3 k_i \int_0^z P_i(t, \sigma) d\sigma\right). \quad (10)$$

All other aspects of the multiple species model are the same as the single-species model described before.

2.3 Model description

The numerical implementation of the equations described in section 2.2 is developed by the Institute for Marine and Atmospheric research Utrecht (IMAU) by *de Bie* [2011] and has the same structure as the schematic overview (Fig. 2). Seasonal and daily variations of incident light have been implemented.

The system is made dimensionless making the results independent of the units being used. Central differencing schemes were used to make the time and space differential and integral terms discrete. Furthermore, for time integration a fourth order Runge-Kutta method was applied³. The model was finalised by checking three different stability criteria:

- The Courant number⁴ $\sigma_c \leq 1$
- The diffusion parameter⁴ $\lambda \leq 1$
- the Peclet number $Pe < 4$

These criteria are necessary to obtain stable solutions.

³Application of this method in fortran is described in *Press et al.* [1992]

⁴[*Vreugdenhil*, 1989]

2.4 New aspects

Two extra phytoplankton species have been added for which the following parameter values can be set:

- growth rate;
- mortality rate;
- sinking velocity;
- nutrient content;
- half saturation value of light-limited growth;
- half saturation value of nutrient-limited growth.

Another parameter has been added to be able to switch between two different light variations:

Seasonal variation in light (see Fig. 2.4):

$$I_{in} = \hat{I}(\cos(lat) \cos(\delta) + \sin(lat) \sin(\delta)). \quad (11)$$

Here \hat{I} is the maximum incident light intensity (see Table 1) and lat is the latitude in radians and δ is the declination angle of the sun, which is given by:

$$\delta = \arcsin \left(0.39795 \cos \left(\frac{0.98563(t - 173)}{180\pi} \right) \right). \quad (12)$$

Where t is given in days. This means at $t=173$ days, δ is maximum (the start of the summer).

Seasonal and daily variation in light:

$$I_{in} = \hat{I}(\cos(lat) \cos(\delta) + \sin(lat) \sin(\delta) \text{varyd}). \quad (13)$$

This is the same equation as the one for seasonal variation but multiplied by the function *varyd* which is defined as:

$$\text{varyd} = \cos(2\pi t + \pi). \quad (14)$$

From Eq. 14 it can be noted that I_{in} can also be negative. To compensate for anomalies like negative phytoplankton growth, the model sets the phytoplankton growth rate to be 0 whenever I_{in} values are negative.

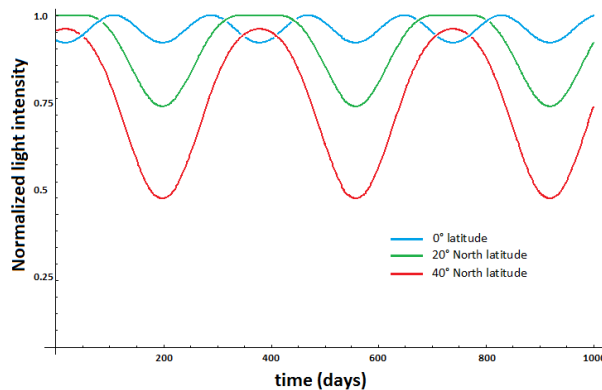


Figure 4: Seasonal cycle of normalized light intensity for 0°, 20° and 40° North latitude.

2.5 Design of experiments

The model is complete and able to compute time series for a maximum of three competing plankton species. The way to address the two research questions is working by the following method. First results will be shown on what happens if the latitude is changed in a seasonal light environment, to see if all species will be able to survive on all latitudes. After that daily variation will be added to the seasonal light environment to see the behavior of the phytoplankton competition in this more realistic scenario.

The first results will be used to answer the first research question - how does competition between 3 phytoplankton species depend on seasonal variation in light at different latitudes? - by looking at the growth behavior of the different species at latitudes of 0, 20 and 40 degrees.

The second part of the results will address the second question - what happens to phytoplankton competition when daily variation is added to a seasonal light environment? - by comparing the new growth behavior to the situation with only seasonal light variability. A table on the next page shows all parameters used by the model and their respective values. These are the default settings of the program.

Parameter values and interpretations¹

Symbol	Interpretation	Units	Value
Independent variables			
t	Time	s	-
z	Depth	m	-
Dependent variables			
P	Population density	$cells\ m^{-3}$	-
I_{in}	Incident light intensity	$\mu mol\ photons\ m^{-2}\ s^{-1}$	-
N	Nutrient concentration	$mmol\ nutrient\ m^{-3}$	-
Parameters			
Lat	Latitude	<i>Degrees N</i>	20
\hat{I}	Maximum incident light intensity	$\mu mol\ photons\ m^{-2}\ s^{-1}$	600
K_{bg}	Background turbidity	m^{-1}	4.5×10^{-2}
k	Absorption coefficient	$m^2\ cell^{-1}$	6×10^{10}
D	Depth of the water column	m	300
κ	Vertical turbulent diffusivity	$m^2\ s^{-1}$	1.2×10^{-5}
N_B	Nutrient concentration at the bottom	$mmol\ nutrient\ m^{-3}$	10
m	Mortality rate	s^{-1}	2.78×10^{-6}
α	Nutrient content of phytoplankton	$mmol\ nutrient\ cell^{-1}$	10^{-9}
ε	Nutrient recycling coefficient	<i>dimensionless</i>	0.5
Species dependent parameters			
$\mu_{max,1}$	Maximum specific growth rate, species 1 (red)	s^{-1}	1.11×10^{-5}
$\mu_{max,2}$	Maximum specific growth rate, species 2 (green)	s^{-1}	1.11×10^{-5}
$\mu_{max,3}$	Maximum specific growth rate, species 3 (blue)	s^{-1}	1.11×10^{-5}
$H_{I,1}$	Half-saturation constant of nutrient limited growth, species 1 (red)	$mmol\ nutrient\ m^{-3}$	4.25×10^{-2}
$H_{I,2}$	Half-saturation constant of nutrient limited growth, species 2 (green)	$mmol\ nutrient\ m^{-3}$	1.65×10^{-2}
$H_{I,3}$	Half-saturation constant of nutrient limited growth, species 3 (blue)	$mmol\ nutrient\ m^{-3}$	1.50×10^{-2}
$H_{N,1}$	Half-saturation constant of light limited growth, species 1 (red)	$\mu mol\ photons\ m^{-2}\ s^{-1}$	20
$H_{N,2}$	Half-saturation constant of light limited growth, species 2 (green)	$\mu mol\ photons\ m^{-2}\ s^{-1}$	25
$H_{N,3}$	Half-saturation constant of light limited growth, species 3 (blue)	$\mu mol\ photons\ m^{-2}\ s^{-1}$	98
v_1	Sinking velocity, species 1 (red)	$m\ s^{-1}$	1.17×10^{-5}
v_2	Sinking velocity, species 2 (green)	$m\ s^{-1}$	1.17×10^{-5}
v_3	Sinking velocity, species 3 (blue)	$m\ s^{-1}$	² 1.17×10^{-6}

Table 1.

¹Unless otherwise specified these are the input values for the model.²This is no typing error!

3 Results

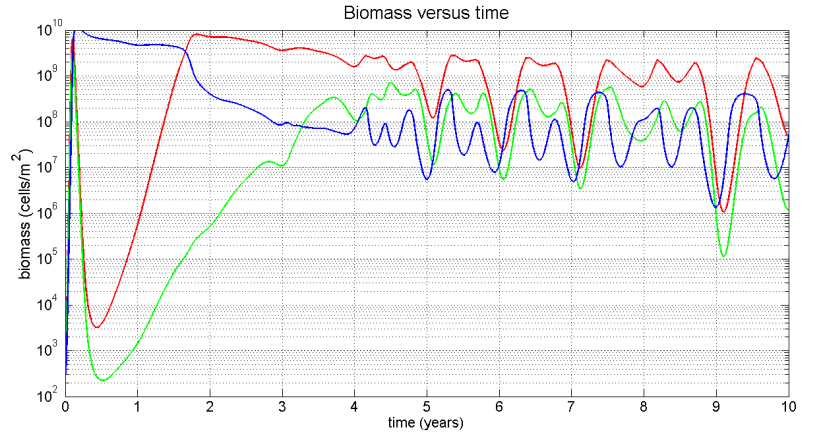
Three species will be indicated by colors: Species 1 (Red), species 2 (Green) and species 3 (Blue). The parameters which are different for the tree plankton species are shown in table 1.

As initial condition, the water column has a well mixed supply of nutrients and a small amount of the three phytoplankton species. The figures in this section show the first 10 years of the phytoplankton model. This is enough time for the phytoplankton to go through their initial perturbation and come state of co-existence. The reason this time frame is highlighted is because it will already be clear at this stage whether a plankton species will survive or not.

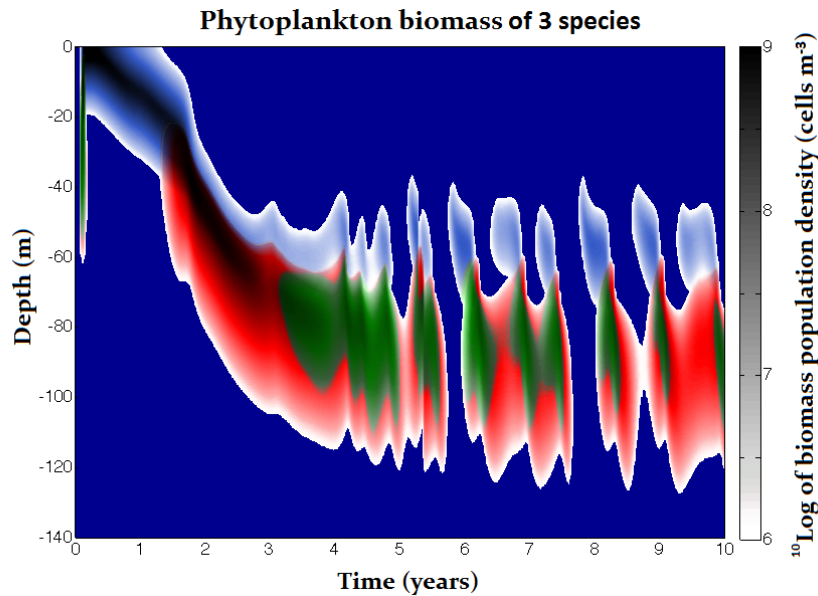
Section 3.1 will show the results for light variation in a seasonal environment. Section 3.2 will show the results for light variation in a seasonal environment with daily variation included.

3.1 Seasonal variation at different latitudes

3.1.1 Default case, 20° N



(a)

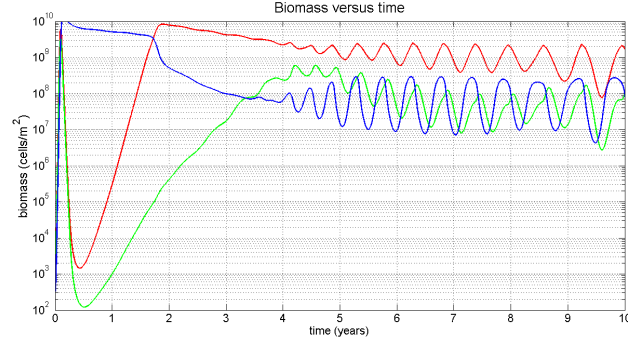


(b)

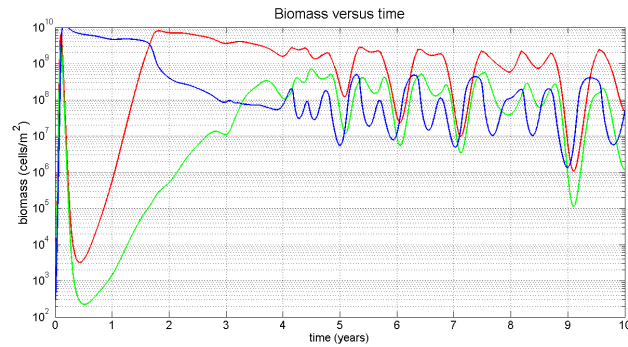
Figure 5: Model simulation with 3 phytoplankton species at 20 degrees north latitude.

The latitude of 20° north is presented first because this is the same location as *Huisman et al.* [2006] used in his research, making it easily comparable. Fig. 5 shows results of the first 10 years after initialisation. Panel (a) of Fig. 5 shows a logarithmic plot depicting depth integrated biomass vs time and panel (b) shows a logarithmic density plot depicting where the biomass is located in the water column over time with species 1 (Red), species 2 (Green) and species 3 (Blue), darker colors indicate higher values for phytoplankton density. In general, the red species has the highest concentration and is situated in the lower regions of the water column, along with the green species which is present in smaller concentrations. The blue species is living in the higher regions of the water column.

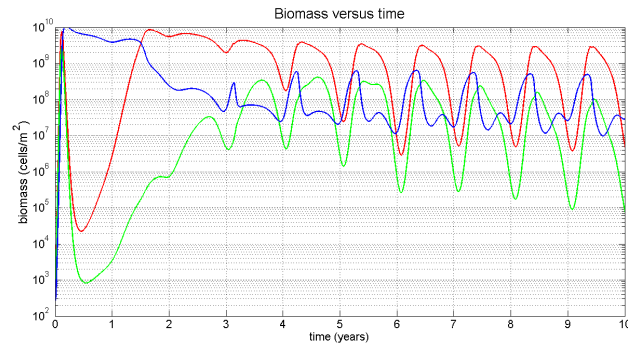
3.1.2 0°, 20° and 40° North



(a) 0° north.



(b) 20° north.



(c) 40° north.

Figure 6: Time series of the total depth integrated biomass of species 1 (Red), species 2 (Green) and species 3 (Blue) at different latitudes.

Fig. 6 shows logarithmic plots of depth integrated phytoplankton biomass over time for the first 10 years after initialisation. It shows that initially the blue species has the highest concentration. After about two years the growth of the red and green species catches up to the blue species resulting in a co-existence where the red species is present in the highest concentrations. Note the similarities in qualitative behavior as at all latitudes three species will survive. Quantitatively there are some differences. At higher latitudes the oscillations have a higher amplitude.⁵

⁵This is because at higher latitudes the difference between summer and winter is larger. At high latitudes the phytoplankton populations reduce to less in the winter, leaving more nutrients in the water column for the next year.

3.2 Seasonal and daily light variation

3.2.1 Default case, 20° N

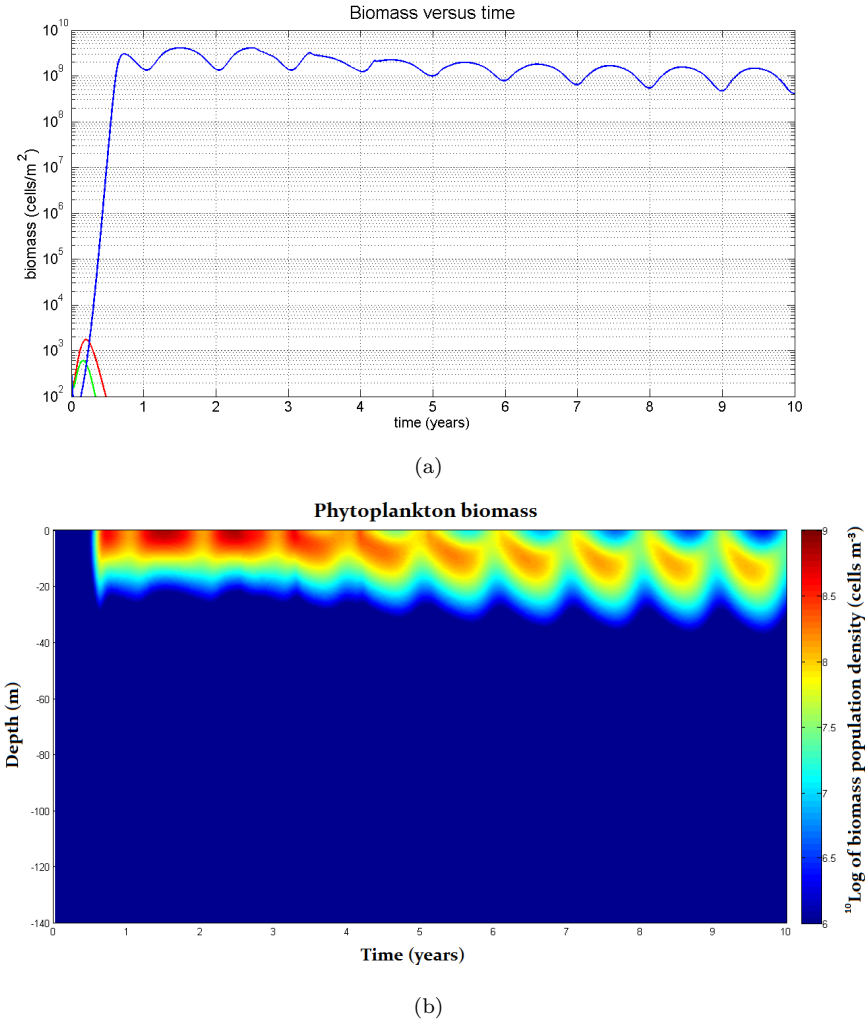
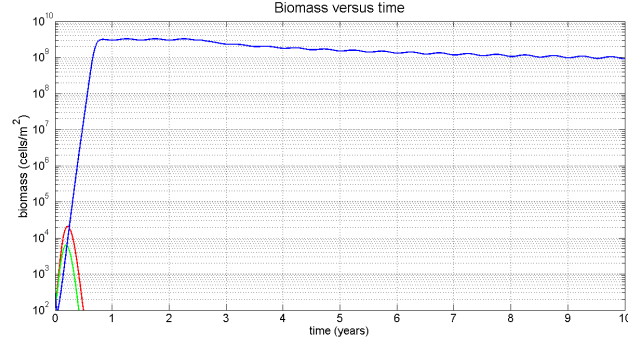


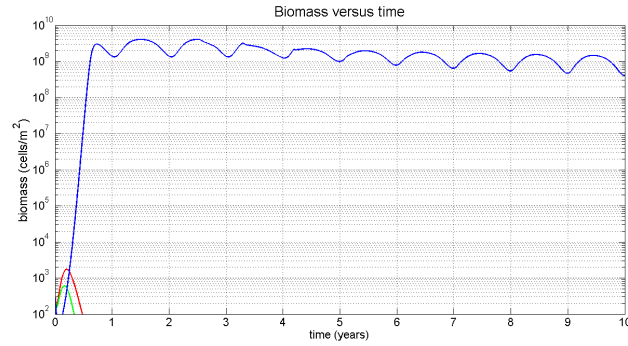
Figure 7: Model simulation with 3 phytoplankton species at 20 degrees north latitude.

Fig. 7 shows results of the first 10 years after initialisation. Panel (a) of Fig. 5 shows a logarithmic plot depicting depth integrated biomass vs time and panel (b) shows a logarithmic density plot depicting where the biomass is located in the water column for species 3 (Blue). Species green and blue are omitted from this plot because their biomass concentration never reaches high enough values to be shown. Red shifted colors indicate higher values for phytoplankton density whereas blue colors indicate small plankton densities. Initially all species grow, but within a time period of about half a year the blue species becomes dominant causing a shading effect and killing the red and the green species.

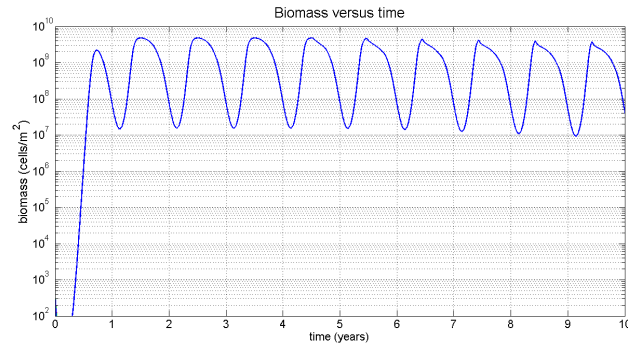
3.2.2 0°, 20° and 40° North



(a) 0° north.



(b) 20° north.



(c) 40° north.

Figure 8: Time series of the total depth integrated biomass of species 1 (Red), species 2 (Green) and species 3 (Blue) at different latitudes.

Fig. 8 shows logarithmic plots of depth integrated phytoplankton biomass over time for the first 10 years after initialisation. Initially all species grow, but within a time period of about half a year the blue species becomes dominant causing a shading effect and killing the red and the green species at all latitudes. Note the similarities in qualitative behavior as two of the plankton species will die out in the first year at all latitudes. Quantitatively, there is a difference. At higher latitudes the dying species will die even faster. This is because the model starts in the winter which has less light at higher latitudes.

4 Discussion

4.1 Seasonal variation at different latitudes

4.1.1 Default case, 20° N

In this scenario of Fig. 5(a), co-existence of three phytoplankton species is visible. After initialisation, the red and the green species quickly drop in numbers because light is absorbed by the slower sinking blue species, limiting their growth. But after just a year the blue species has sunk enough to allow light to penetrate through to the red and green species resulting in their growth. After approximately 5 years a more or less periodic co-existence will appear allowing all three species to survive. Fig. 5(b) shows how the blue species is sinking more slowly and therefore reducing the light at higher depths where the red and green species have already sunk to. Even in the co-existing end state the blue species is visible at a lower depth than the other two species, which reside at the same depth. This shows that sinking velocity plays an important role in the settling depth of phytoplankton.

4.1.2 0°, 20° and 40° North

Apparently phytoplankton can co-exist at a latitude of 20° north under seasonal light conditions. To see if this holds for other latitudes Fig. 6 shows the same phytoplankton at different latitudes. At all latitudes, the general behavior is the same as at 20° north, but a slight variation in quantities is visible. Higher latitudes result in a larger difference between summer and winter biomass densities. This is not surprising considering that higher latitudes receive less sunlight overall than lower latitudes. A surprising fact however is that at higher latitudes the maximum density is slightly higher. This is explained by the fact that light gradients are stronger, the difference between winter and summer is larger. This means that plankton exist in a smaller period of time but will still be in the same abundance because their growth rate does not change. This results in a higher phytoplankton concentration at higher latitudes.

4.2 Seasonal and daily light variation

The effect of light reduction by a factor 2 explained:

When daily light is added to a seasonal environment, the total amount of light received over a certain period of time is reduced to half. This is because without daily light variation there is no night. With daily light variation is added, half of the time it will be night so phytoplankton will not be able to grow at all at this time. This effect is independent of latitude, as summers will have longer days and winter will have shorter days on higher latitudes.

4.2.1 Default case, 20° N

In the scenario where daily variation in light is added to the already existing seasonal cycle, Fig. 7(a) shows us that the same phytoplankton as in the seasonal case are not all visible anymore. The red and the green species die out almost instantaneously, leaving only the blue species to survive. This is the result of the blue species shading the red and the green species. The lower sinking velocity of the blue species causes it to stay on top for such a long time that the red and green phytoplankton can not grow enough to be able to get through the first winter⁶. A periodic solution for the blue phytoplankton species is already present one year after initialisation.

4.2.2 0°, 20° and 40° North

Maybe a change in latitude will yield a situation where the red and green species have enough time to develop and get through their first winter. Fig. 8 shows the different latitudes next to each other. The red and green species still will not make it. At 0°, these species are able to grow a little larger than on 20°, but still by far not enough to even come close to the blue species. At 40°, light is already limited so gravely that the red and blue plankton species do not even show up on the graph, they plummet into nonexistence.

⁶This may be a result of the initial conditions of the model as it starts at midnight on January 1st. This has not been tested though, leaving it to be an interesting subject for further research.

4.3 Future research

Research into phytoplankton will remain an important subject. The model used for this thesis is only describing a segment of all parameters that influence phytoplankton behavior. In the future a lot of other things could be added to the model giving more and more detailed results. Research subjects to consider are:

- Changing the initial time of the model to the spring or the summer may give the two dying plankton species just enough light to grow through the next winter.
- Making the model **account for more dimensions** would make it much more valuable for calculations on coastal regions and estuaries.
- Using C or C++ instead of Fortran90 to increase the computational efficiency.
- Adding detritus and zooplankton - research done by *Luo et al.* [2012] - added to this model, would give a more complete overview of a plankton system.

5 Conclusions

Revisiting the first research question:

- *How does competition between 3 phytoplankton species depend on seasonal variation in light at different latitudes?*

All present phytoplankton species are able to exist alongside each other at all latitudes. This means that variation in the light intensity of different latitudes does not influence the way phytoplankton are able to live together.

Revisiting the second research question:

- *What happens to phytoplankton competition when daily variation is added to a seasonal light environment?*

By combining the two results for the different cases of seasonal and seasonal plus daily light variation this research comes to the following conclusion:

The reduction of in a seasonal environment causes the phytoplankton species with the higher sinking velocities to die. They do not receive enough light anymore to come to a stable existence. This happens at all latitudes, showing that the dying of two plankton species is related to the day-night variation and not a result of changing light intensity.

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