Spectral formulation of the critical depth theory

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SPECTRAL FORMULATION OF THE CRITICAL DEPTH THEORY

Master thesis

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Zahvale

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Sažetak:
Fitoplankton predstavlja skupinu biljnih planktona koji mogu živjeti u površinskom osunčanom sloju oceana. Za preživljavanje fitoplanktona potrebna je svjetlost i hranjive tvari. Ova skupina planktona ima važnu ulogu u morskom ekosustavu zbog fotosinteze (primarne proizvodnje) pri kojoj dolazi do asimilacije ugljika. Intenzitet svjetlosti u oceanu eksponencijalno opada s dubinom ovisno o optičkim svojstvima morske vode, ali i o količini planktona u moru. U ovom radu opisane su osnove natjecateljskog modela, teorije kritične dubine i modela primarne proizvodnje. Rad također opisuje matematički formalizam koji pokazuje kako se dobije izraz za vremensku evoluciju biomase fitoplanktona izveden iz advekcijsko-difuzijsko-reakcijske jednadžbe. U radu su opisana dva modela: monokromatski model za jednu, dvije i više populacija fitoplanktona te spektralni model za jednu i dvije populacije fitoplanktona. Na kraju rada opisan je natjecateljski model za fitoplanktone koji pokazuje koja će vrsta preživjeti te mogu li dvije vrste koegzistirati u oceanu.

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Master thesis

SPECTRAL FORMULATION OF THE CRITICAL DEPTH THEORY

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University graduate study programme Physics, orientation Environmental Physics

Abstract:

Phytoplankton is a group of plant plankton that can live in the uppermost sunlight ocean. It requiers ocean light and nutrients to sustain itself. This group of plankton plays a major role in the ocean ecosystem due to the process of photosynthesis (primary production) in which carbon assimilation occurs. The intensity of light in the ocean decreases exponentially with depth with the rate of decrease determined by the optical properties of seawater, which are also determined by the amount of plankton in the sea. This work describes the basics of a competition model, critical depth theory and a primary production model. The work also describes mathematically how the expression for the temporal evolution of phytoplankton biomass in time is derived from an advection-diffusion-reaction equation. In this work two models are described: monochromatic model for one, two and N phytoplankton populations and a spectral model for one and two phytoplankton populations. At the end of the work, a competition model for phytoplankton is described which predicts which species will survive and whether both species can coexist in the ocean.

Keywords:

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Contents

1 Introduction

Phytoplankton (plant plankton) are free-floating autotrophic organisms living in ocean. The word phytoplankton was first used by the German scientist Victor Heusen in 1887 and comes from the Greek word "phyton" which means plant, and "planktos" which means wanderer or tramp. These organisms first appeared two billion years ago. Phytoplantkon is found in the surface illuminated layer of the ocean where there is enough sunlight needed for photosynthesis. Phytoplankton actively participate in the carbon cycle due to carbon assimilation in photosynthesis. Phytoplankton biomass contains only one percent of the carbon of the entire biosphere, and the life cycle of phytoplankton is much shorter than the life cycle of terrestrial plants. It is therefore extremely sensitive to changes in the environment, but it is also an enviromental regulator due to the enormous carbon flow in global primary production. Phytoplantkon form the basis of the food chain in rivers, seas and oceans. Their photosynthetic activity is responsible for almost 50 % of global primary production.

The regulation of the environment is also influenced by man (anthropogenic influence). According to some theories, oil is formed after dead organisms such as plankton remain trapped beneath sedimentary rocks exposed to high pressure and temperature. Nowadays, the carbon stored in these deposits is used as fuel and released into the atmosphere which affects climate change. Primary production process removes carbon dioxide and releases oxygen. Phytoplankton that sinks to the seabed consequnetly reduces the concentration of carbon in the atmosphere. This process is called "the biological pump". Global phytoplankton primary production is estimated at about 50 PgC per year, of which about 8 % is needed to maintain the total annual world fishing efforts. With the above we see that the research of primary production of the oceans and seas is of great interest for fisheries and the study of the climate system. Since the surface of the ocean is huge, research of the primary production necessarily involves measuring and modelling the process itself, for which different approaches have been developed.

In 1953 Norwegian oceanographer and meteorologist H. U. Sverdrup published an article [1] in which he proposed the concept of the critical depth to explain the initiation of the spring bloom in the North Atlantic. Considering the work before him, Sverdrup was the first to make a mathematical model of critical depth theory. Sverdrup's model was among the first models to explore physical - biological interactions in the ocean. His work has now been applied, adapted and tested across many aquatic systems worldwide.

Critical depth theory uses the following assumptions:
1) Whithin the surface layer turbulance is strong enough to distributes the plankton homogeneously through the layer.
2) Whithin the mixed layer photosynthesis is not limited by a lack of nutrients.
3) The production of organic matter by photosinthesis is proportional to the light energy at depth.

Using the above assumptions we can obtain an expression for the critical depth. The exact value of critical depth depends on the incoming solar radiation, amongst other things.

There are two different parts of the critical depth concept that Sverdrup proposes [2]: the first part deals with the use of the law of conservation of mass in the water column to calculate the change in the amount of phytoplankton concentration. In this part he uses formulas (known before his work, proposed by Gran and Braarud in 1935) which are axiomatic (taken as correct whithout testing). The second part refers to the study of the main factors responsible for the formation of blooms (these are hypotheses amenable to testing). In general, we can say that in Svedrup's model the biological dynamics in the ocean is described by equations which are based on the principles of the law of conservation of mass (mass balance).

There are three important depths that need to be mentioned in this work [2]:
1) Critical depth (biological depth horizon) is the depth to which phytoplantkon can be sustained.
2) Mixing depth or mixed layer depth is the depth of active mixing.
3) Euphotic depth is the depth to which light can penetrate.

Based on Sverdrup's work, models were made that gave a new perspective on phytoplankton dynamics and various factors responsible for phytoplankton blooms. Phytoplantkon blooms have been described as periods of rapid (explosive) growth in phytoplantkon biomass. It is important to note that some blooms are fast (happen quickly, have short periods), while some blooms are long lasting (have long periods). Blooms are actually a condition of elevated (increased) phytoplantkon concentrations. The concentration of the photosynthetic pigment chlorophyll (Chl) is taken as a measure of phytoplankton concentration. It can be detect from space.

One of the processes that is of societal importance and is related to primary production is upwelling. Upwelling is an oceanographic phenomenon that involves wind-driven motion of dense, cooler, and usually nutrient-rich water from deep water towards the ocean surface, replacing the warmer, usually nutrient-depleted surface water. The nutrient-rich upwelled water stimulates the growth and reproduction of primary producers such as phytoplankton. Due to the biomass of phytoplankton and presence of cool water in these regions, upwelling zones can be identified by cool sea surface temperatures (SST) and high concentrations of chlorophyll-a. [3]

The idea of this work is to apply Sverdrup's model to a monochromatic and a spectral model for phytoplankton competition. We begin with a basic competition model for two species.

In Table 1 all parameters and variables used in monochromatic and spectral model for phytoplankton populations are listed.

Table 1: *Parameters and variables used in this work.*

Variable's name	**Variable's mark**	**Variable's unit**
Primary production	$P = P(z,t)$	$\mathrm{mgC\,m^{-3}\,h^{-1}}$
Primary production for each population	$P_i = P_i(z,t)$	$\mathrm{mgC\,m^{-3}\,h^{-1}}$
Phytoplankton biomass	$B = B(z,t)$	$\mathrm{mgChl\,m^{-3}}$
Phytoplankton biomass for each population	$B_i = B_i(z,t)$	$\mathrm{mgChl\,m^{-3}}$
Irradiance (light intensity)	$I = I(z,t)$	$\mathrm{W\,m^{-2}}$
Two spectral bands of irradiance	$I_1 = I_1(z,t), I_2 = I_2(z,t)$	$\mathrm{W\,m^{-2}}$
Attenuation coefficient	$K = K(z,t)$	$\mathrm{m^{-1}}$
Optically uncoupled critical depth	$C = const.$	m
Optically coupled critical depth	$S = S(t)$	m
Parameter's name	**Parameter's mark**	**Parameter's unit**
Surface irradiance	$I_0 = const.$	$\mathrm{W\,m^{-2}}$
Loss (mortality) rate	$L = const.$	$\mathrm{s^{-1}}$
Loss rate for each population	$L_i = const.$	$\mathrm{s^{-1}}$
Mixed layer depth	$z_m = const.$	m
Critical depth	$z_c = const.$	m
Initial slope (growth rate)	$\alpha = const.$	$\mathrm{mgC\,(mgChl)^{-1}\,W^{-1}\,m^{-2}\,h^{-1}}$
Initial slope for each population	$\alpha_i = const.$	$\mathrm{mgC\,(mgChl)^{-1}\,W^{-1}\,m^{-2}\,h^{-1}}$
Seawater attenuation coefficient	$K_W = const.$	$\mathrm{m^{-1}}$
Specific attenuation coefficient	$k_B = const.$	$\mathrm{m^{2}\,(mgChl)^{-1}}$
Specific attenuation coefficient for each population	$k_{Bi} = const.$	$\mathrm{m^{2}\,(mgChl)^{-1}}$
Initial phytoplankton biomass	$B_0 = const.$	$\mathrm{mgChl\,m^{-3}}$
Number of populations	$N = const.$	-
Index of population	$i = 1, ..., N$	-
Time index	n	-
Depth	z	m
Time	t	h
Time step	Δt	h
Diffusion coefficient	D	$\mathrm{m^{2}\,s^{-1}}$

2 Competition model

In this model [4], the subject of observation are two species which compete for the same limited food source or in some way inhibit each other's growth. Using 2-species Lotka-Volterra competition model we obtain the change in quantity of each species (N_1 and N_2) over time [4]:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right), \tag{2.1}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2}\right), \tag{2.2}$$

where r_1 and r_2 are the linear birth rates, K_1 and K_2 are the carrying capacities (enviromental capacities) and b_{12} and b_{21} are measures of the competitive effect of N_1 and N_2. It is useful to introduce the substitutions:

$$u_1 = \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \quad a_{12} = b_{12}\frac{K_2}{K_1}, \quad a_{21} = b_{21}\frac{K_1}{K_2}. \tag{2.3}$$

Now equations (2.1) and (2.2) become:

$$\frac{du_1}{d\tau} = u_1\left(1 - u_1 - a_{12}u_2\right) = f_1(u_1, u_2), \tag{2.4}$$

$$\frac{du_2}{d\tau} = \rho u_2\left(1 - u_2 - a_{21}u_1\right) = f_2(u_1, u_2). \tag{2.5}$$

The steady states are solutions for which $f_1(u_1, u_2) = f_2(u_1, u_2) = 0$.

On Figure 1 we can see four different situations in the phase space for various cases of a_{12} and a_{21}. Blue and orange lines are called nulclines and they represent steady states of equations (2.4) and (2.5).

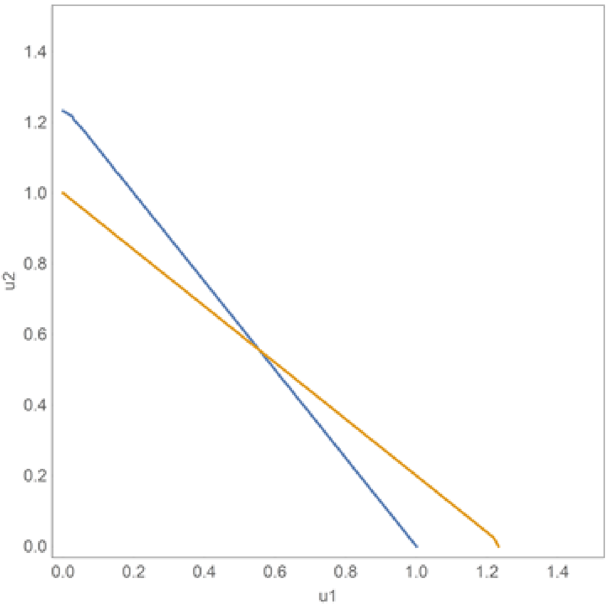
In the first case, shown in Figure 1a), where $a_{12} < 1$ with $a_{21} < 1$ there is a stable steady state where both species coexist. For example, if carrying capacities K_1 and K_2 are the same and interspecific competition is $b_{12} < 1$ and $b_{21} < 1$, then the two species have low population size (competition is not aggresive which means that one population will not be exterminated). On Figure 1a) points on the u_1 axis are $(1, 0)$ and $(0, 1/a_{21})$ and on the u_2 axis are $(0, 1)$ and $(0, 1/a_{12})$, where points are defined as (u_1, u_2). If the b_{12} and b_{21} are about the same and the K_1 and K_2 are different, it is not easy to say what will happen.

In the second case, shown in Figure 1b), where $a_{12} > 1$ and $a_{21} > 1$, if the K's are about equal, then the $b_{12} > 1$ and $b_{21} > 1$.

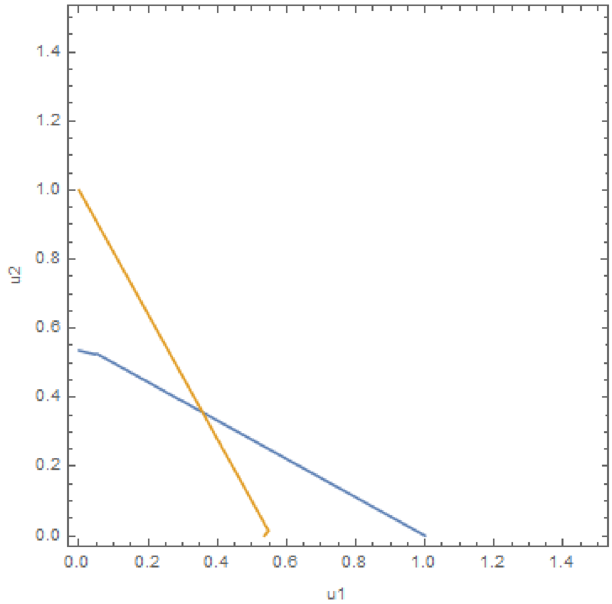
In the third case, shown in Figure 1c), in which the interspecific competition of one species is much stronger than the other ($b_{21} >> b_{12}$), or the carrying capities are sufficiently different ($K_1 \neq K_2$), the result is that u_1 species dominates and the other species u_2 dies out.

In the fourth case, shown in Figure 1d), in which the interspecific competition of one species is much stronger than the other ($b_{12} >> b_{21}$), or the carrying capities are sufficiently different ($K_1 \neq K_2$), the result is that u_2 species dominates and the other species u_1 dies out.

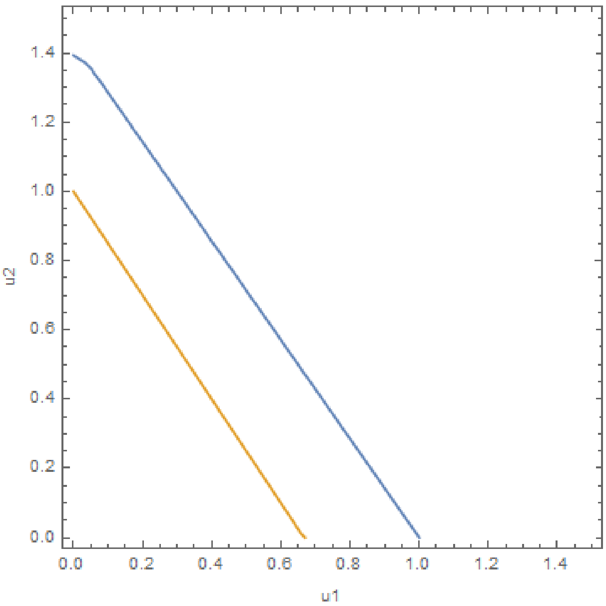
(a) *Case when* $a_{12} < 1$ *and* $a_{21} < 1$



(b) *Case when* $a_{12} > 1$ *and* $a_{21} > 1$



(c) *Case when* $a_{12} < 1$ *and* $a_{21} > 1$



(d) *Case when* $a_{12} > 1$ *and* $a_{21} < 1$

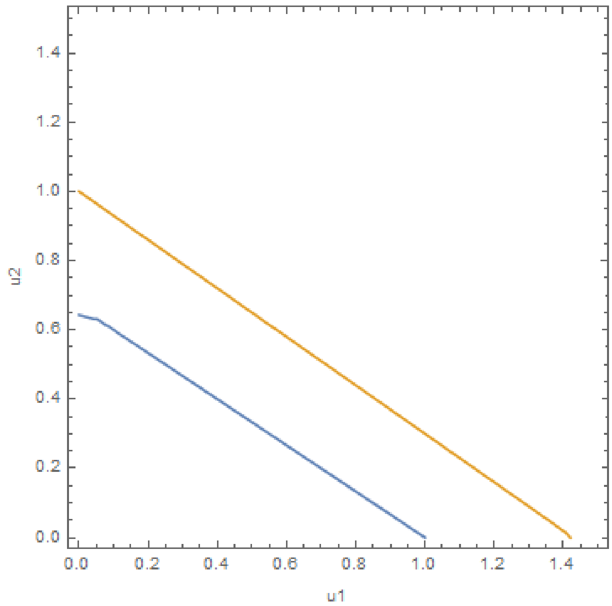


Figure 1: *Phase plane for the various cases of* a_{12} *and* a_{21}. *Blue curve represents steady state for equation* (2.4)*, orange curve represents steady state for equation* (2.5).

3 Primary production model

Phytoplantkon primary production P is defined as rate of anorganic carbon assimiliaton by phytoplantkon. Generally, primary production depends on time (t) and depth (z). **Chlorophyll concentration** is used as a measure of **phytoplantkon biomass** B. Primary production depends of avaliable light and is defined as:

$$P = \alpha I, \tag{3.1}$$

where α is initial slope and I is light intensity (irradiance). **Irradiance** is taken as a meassure of available sunlight and is defined as a light energy that in units of time passes through a unit area perpendicular to the direction of light propagation. Generally, irradiance is a function that depends on time (t) and depth (z). Beer-Lambert law dictates that irradiance decreasses exponentially with depth:

$$I = I_0 e^{-Kz}, \tag{3.2}$$

where I_0 is surface irradiance and K is the attenuation coefficient which shows the rate of decline of the amount of light in the sea.

Figure 2 respresents irradiance as function of depth mentioned in equation (3.2) and primary production as function of depth mentioned in equation (3.1). It can be seen that the primary production and irradiance decrease exponentially with depth. Used surface irradiance I_0 is 350 Wm^{-2}, intial slope α is $0.2\ \mathrm{mgC(mgChl)^{-1}W^{-1}m^{-2}h^{-1}}$ and attenuation coefficient K is 0.04 m^{-1}.

In the open ocean the attenuation coefficient depends on biomass concentration:

$$K = K_w + k_B B, \tag{3.3}$$

where K_w is seawater attenuation coefficient representing light atenuation processes due to scattering and apsorption of particles and solutes, k_B is specific phytoplankton attenuation coefficient representing light attenuation processes due to apsorption and scattering by phytoplankton.

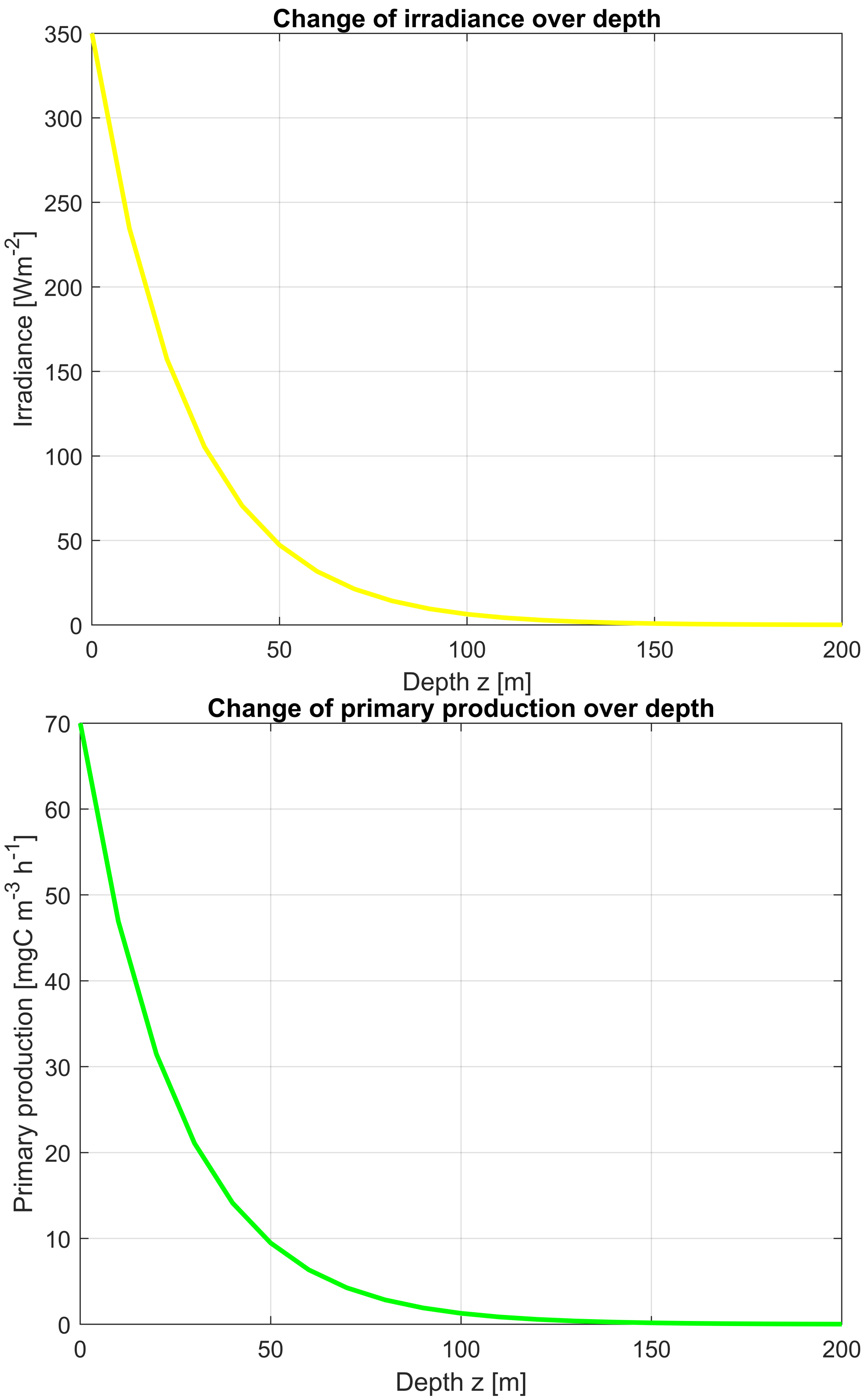


Figure 2: *Change of irradiance (yellow curve) and primary production (green curve) over depth in a primary production model.*

4 Critical depth theory

In 1953 Harald Urlik Sverdrup set up a simple mathematical model based on a water column that connects the roles of vertical water mixing, light attenuation with depth and seasonal increase in light. The Sverdrup's model is a model based on an earlier one proposed by Riley [5] in 1946. Gordon Arthur Riley was an American biological oceanographer who studied the dynamics of plankton ecosystems. The critical depth hypothesis is the solution of Sverdrup's model. This hypothesis predicts that blooms begins when seasonally mixed layer is shallower than the critical depth z_c.

The model rests on the following assumptions [6]:
1) Phytoplankton growth rate is proportional to the light intensity ($\alpha \propto I$).
2) The light extintion coefficient (atenuation coefficient) K is constant (K = const.).
3) Phytoplankton loss rate is constant (L = const.).
For light intensity Sverdrup used Beer-Lambert's law:

$$I = I_0 e^{-Kz}, \tag{4.1}$$

where I_0 is surface irradiance required for the photosynthesis process.

Sverdrup's model can be understood in terms of differential equation for the time evolution of phytoplankton concentration (biomass) B [6]:

$$\frac{\partial B}{\partial t} = (\alpha - L)B + \frac{\partial}{\partial z}\left(D\frac{\partial B}{\partial z}\right), \tag{4.2}$$

where α is the rate of phytoplankton growth, L is phytoplankton loss rate and D is the vertical mixing coefficient (diffusion coefficient).

The assumption that the vertical mixing D is strong enough to evenly distribute the organisms in the ocean's surface mixed layer allows the integration of equation (4.2) from the surface (0) to the bottom of the mixed layer (depth z_m) resulting in the equation (z axis is positive downwards):

$$\frac{\partial \langle B \rangle}{\partial t} = \frac{\alpha I_0}{k z_m}(1 - e^{-kz_m})\langle B \rangle - L\langle B \rangle, \tag{4.3}$$

where $\langle B \rangle$ is the average phytoplankton biomass (over depth):

$$\langle B \rangle = \int_0^{z_m} B dz. \tag{4.4}$$

Setting $\frac{\partial\langle B\rangle}{\partial t} = 0$, an equation is obtained for the critical depth z_c for which the integral over depth of growth is equal to the integral over depth of loss:

$$\frac{\alpha I_0}{K z_c}(1 - e^{-K z_c}) = L. \tag{4.5}$$

The value of z_c depends on 4 model parameters: α, L, k and I_0. If $z_c > z_m$ the phytoplankton can be sustained in the mixed layer, if $z_c < z_m$ it can not.

5 Monochromatic model

5.1 Monochromatic model with one phytoplankton population

In order to obtain the expression for the time evolution of phytoplankton biomass in the mixed-layer, it is necessary to integrate the advection-diffussion-reaction equation by depth:

$$\frac{\partial B}{\partial t} + w\frac{\partial B}{\partial z} = D\frac{\partial^2 B}{\partial z^2} + PB - LB, \tag{5.1}$$

where $\frac{\partial B}{\partial t}$ is local change of biomass, $w\frac{\partial B}{\partial z}$ is the advection term, $D\frac{\partial^2 B}{\partial z^2}$ is the diffusion term in which D is the diffusion coefficient, $P = P(z,t)$ is primary production which is function of depth z (axis of depth is positive downwards) and time t, $B = B(z,t)$ is phytoplantkon biomass which is also function of depth z and time t. This equation describes the evolution of biomass over time.

Using equations (3.1) and (3.2) primary production $P(z,t)$ is:

$$P = \alpha I = \alpha I_0 e^{-Kz}, \tag{5.2}$$

where K is atenuation coefficient which is defined in equation (3.3). By integrating equation (5.1) from the surface (0) to the base of the mixed layer (z_m) we get:

$$\int_0^{z_m} \frac{\partial B}{\partial t} dz + \int_0^{z_m} w\frac{\partial B}{\partial z} dz = \int_0^{z_m} D\frac{\partial^2 B}{\partial^2 z} dz + \int_0^{z_m} \alpha I_0 e^{-Kz} B dz - \int_0^{z_m} LB dz. \tag{5.3}$$

After integration, the equation (5.3) yields:

$$\frac{\partial \langle B \rangle}{\partial t} z_m + \left(wB - D\frac{\partial B}{\partial z} \right)\Bigg|_0^{z_m} = -\frac{\alpha I_0}{K} e^{-Kz}\Bigg|_0^{z_m} \langle B \rangle - L\langle B \rangle z_m, \tag{5.4}$$

where $\langle B \rangle$ is defined as:

$$\int_0^{z_m} B dz = \langle B \rangle z_m. \tag{5.5}$$

One of the assumptions in this model is that there is no interaction at the boundaries (0 and z_m) which means that flux on the surface and the mixed-layer base is equal to zero:

$$wB - D\frac{\partial B}{\partial z} = 0 \quad \text{for} \quad z = 0, \tag{5.6}$$

$$wB - D\frac{\partial B}{\partial z} = 0 \quad \text{for} \quad z = z_m. \tag{5.7}$$

Equation (5.4) devided by z_m now becomes equation which is recognized as Sverdrup's equation in (4.3):

$$\frac{\partial\langle B\rangle}{\partial t} = \frac{\alpha I_0}{K z_m}\big(1 - e^{-K z_m}\big)\langle B\rangle - L\langle B\rangle. \tag{5.8}$$

Numerical form of equation (5.8) is:

$$B(n+1) = B(n) + \frac{\alpha I_0 \Delta t}{K z_m}\big(1 - e^{-K z_m}\big)B(n) - LB(n)\Delta t, \tag{5.9}$$

where Δt is the time step and n the time index.

We define A as the ratio of surface production to losses (uniform over depth):

$$A = \frac{\alpha I_0}{L}. \tag{5.10}$$

Optically uncoupled critical depth C is the critical depth associated with $k_B = 0$ and is defined as [7]:

$$C = \frac{1}{K_w}\bigg(W_0(-Ae^{-A}) + A\bigg), \tag{5.11}$$

where W_0 is Lambert W function. The optically uncoupled critical depth is independent of time $C \neq C(t)$. Optically coupled critical depth S is the critical depth associated with $k_B \neq 0$ and is defined as [7]:

$$S = \frac{1}{K_w + k_B B}\bigg(W_0(-Ae^{-A}) + A\bigg). \tag{5.12}$$

Optically coupled critical depth is time-depended $S = S(t)$. We now simulate the temporal evolution of phytoplankton biomass B using equation (5.9). Parameters used in this model can be seen in Table 2.

Table 2: *Parameters used in a monochromatic model for one phytoplankton population.*

Parameter	Amount	Unit
I_0	350	$\mathrm{Wm^{-2}}$
L	10	$\mathrm{s^{-1}}$
z_m	150	m
α	0.2	$\mathrm{mgC(mgChl)^{-1}W^{-1}m^{-2}h^{-1}}$
K_W	0.04	$\mathrm{m^{-1}}$
k_B	0.014	$\mathrm{m^2(mgChl)^{-1}}$
B_0	(0.1 - 0.9)	$\mathrm{mgChl\,m^{-3}}$

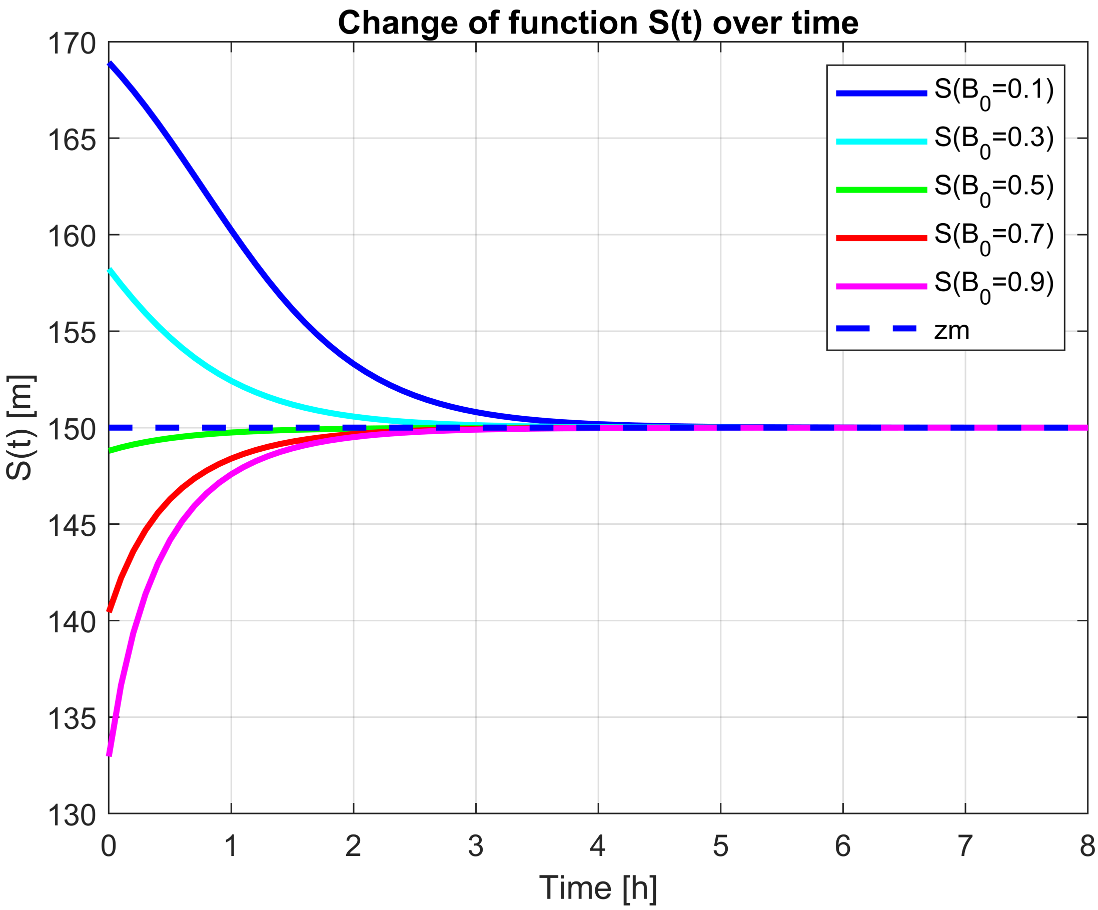


Figure 3: *Change of optically coupled critical depth $S(t)$ over time t in monochromatic model with one phytoplankton population. Blue dashed line shows base of the mixed layer z_m and other lines (blue, green, red and purple full line) show optically coupled critical depth $S(t)$. Different start points of lines correspond to different initial biomass conditions.*

Figure 3 shows that optically coupled critical depth $S(t)$ for one phytoplankton population, regardless of given initial conditions, tends to the base of the mixed layer depth z_m. Curves that take values of initial biomass less than $0.5\ \mathrm{mgChl\,m^{-3}}$ (blue curves) decrease over time to a fixed value of mixed layer depth of $150\ \mathrm{m}$. Curves that take values of initial biomass greater than $0.5\ \mathrm{mgChl\,m^{-3}}$ (green, red and purple line) increase over time to a fixed value of mixed layer depth of $150\ \mathrm{m}$. The duration of this simulation is $8\ \mathrm{h}$ which is sufficient to reach the stabilized value of optically coupled critical depth.

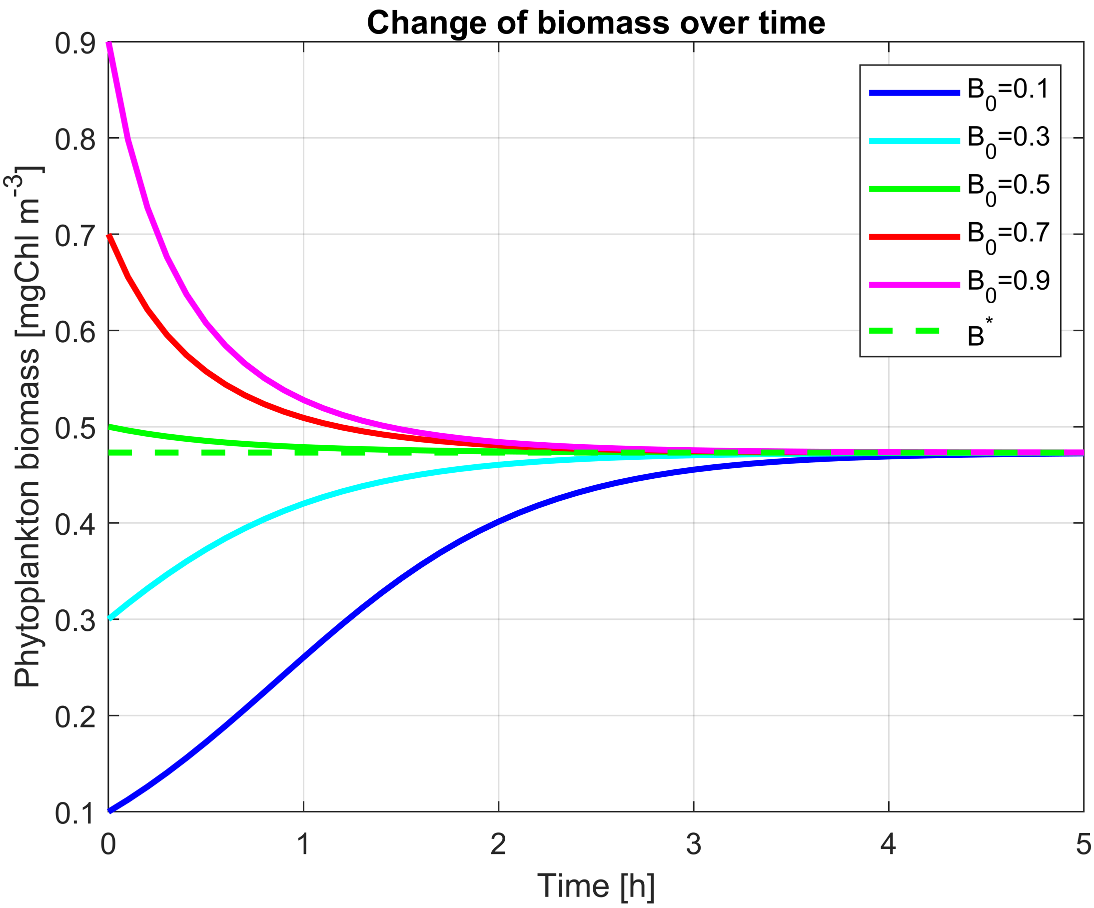


Figure 4: *Change of biomass B(t) over time in a monocromatic model for one phytoplankton population at the mixed layer depth z_m. Green dashed line shows steady-state biomass and other lines (purple, red, green, cyan and blue full line) show change of biomass $B(t)$ over time. Different start points of lines correspond to different initial biomass conditions.*

Figure 4 shows that biomass for one phytoplankton population, regardless of biomass initial conditions, tends to a steady-state biomass given by [7]:

$$B^* = \frac{K_w}{k_B}\left(\frac{C}{z_m} - 1\right). \tag{5.13}$$

Biomass at the begining of simulation is $0.1, 0.3, 0.5, 0.7, 0.9\ \mathrm{mgChl\,m^{-3}}$ (arbitrarily selected values). Curves that use values of initial biomass less than $0.5\ \mathrm{mgChl\,m^{-3}}$ (blue and cyan line) increase over time to a fixed value of steady-state biomass. Curves that used values of initial biomass greater than $0.5\ \mathrm{mgChl\,m^{-3}}$ (green, red and purple line) decrease over time to a fixed value of steady-state biomass. The duration of this simulation is 5 h which is sufficient to reach the stabilized value of biomass.

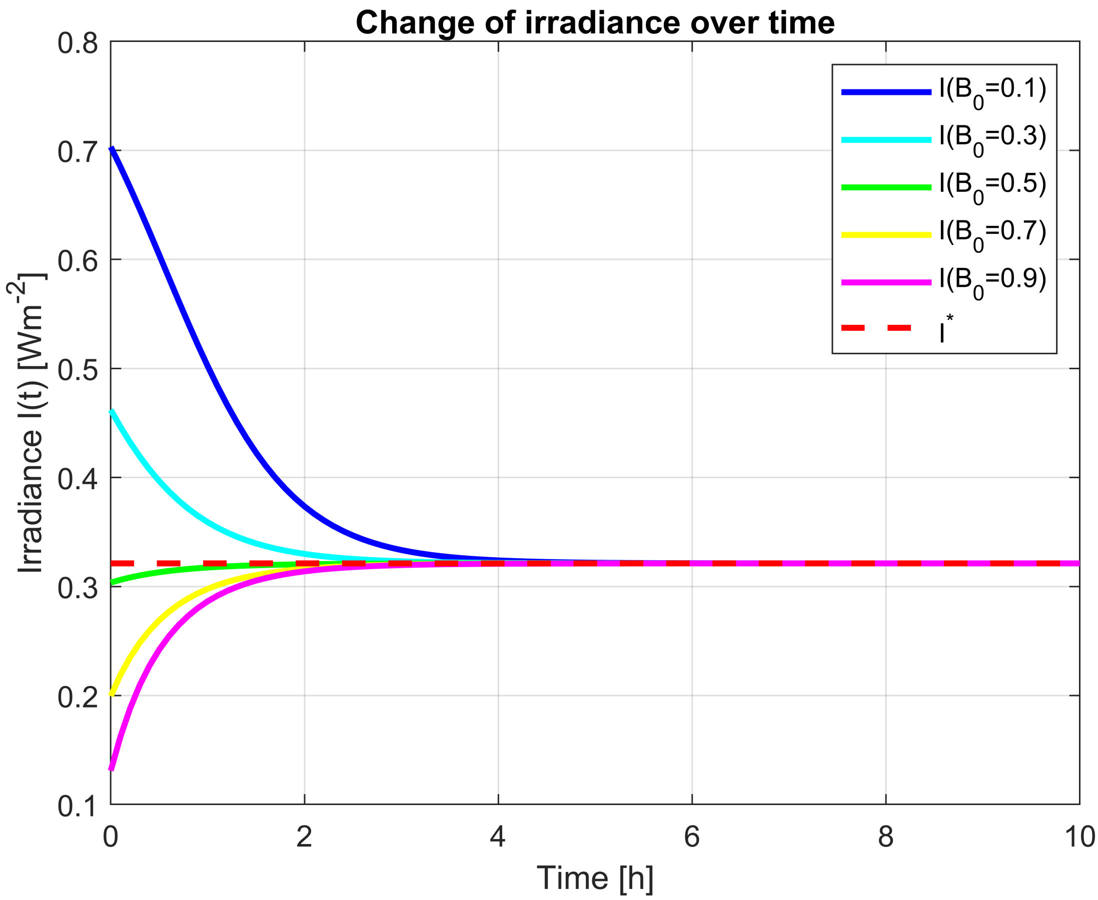


Figure 5: *Change of irradiance $I(t)$ over time t at the mixed layer depth z_m. Red dashed line shows steady-state irradiance I^* and other lines (blue, cyan, green, yellow and purple line) show irradiance $I(t)$. Different start points of lines correspond to different initial biomass conditions.*

Figure 5 shows that irradiance for one population at the base of the mixed layer (z_m) tends to a steady-state irradiance which is defined as:

$$I^* = I_0 e^{-(K_w + k_B B^*) z_m}. \tag{5.14}$$

Steady-state irradiance profile has the same shape as the irradiance profile defined in equation (3.2). The only difference is that this irradiance uses steady-state biomass B^* and mixed layer depth z_m. In Figure 5 curves with values of initial biomass less than $0.5\ \mathrm{mgChl\,m^{-3}}$ (blue and cyan line) decrease over time to a fixed value of steady-state irradiance. Curves with values of initial biomass greater than $0.5\ \mathrm{mgChl\,m^{-3}}$ (green, red and purple line) increase over time to a fixed value of steady-state irradiance.

5.2 Monochromatic model with two phytoplankton populations

The mathematical procedure for two phytoplankton populations is exactly the same as for one population. We will use indices 1 and 2 to indicate population. With two populations we have two advection-diffussion-reaction equations (5.1), one for each population:

$$\frac{\partial B_1}{\partial t} + w\frac{\partial B_1}{\partial z} = D\frac{\partial^2 B_1}{\partial^2 z} + P_1 - L_1 B_1, \tag{5.15}$$

$$\frac{\partial B_2}{\partial t} + w\frac{\partial B_2}{\partial z} = D\frac{\partial^2 B_2}{\partial^2 z} + P_2 - L_2 B_2. \tag{5.16}$$

where B_1 and B_2 are phytoplantkon biomass for each population, P_1 and P_2 are primary production terms for each population, L_1 and L_2 are phytoplankton mortality rate for each population. Primary productions P_1 and P_2 for each population are defined as:

$$P_1 = \alpha_1 I = \alpha_1 I_0 e^{-Kz}, \tag{5.17}$$

$$P_2 = \alpha_2 I = \alpha_2 I_0 e^{-Kz}, \tag{5.18}$$

where α_1 and α_2 are initial slope for each population, K is atenuation coefficient which is now defined as:

$$K = K_w + k_{B1} B_1 + k_{B2} B_2, \tag{5.19}$$

where K_w is seawater attenuation coefficient, k_{B1} and k_{B2} are specific phytoplankton attenuation coefficient for each population. It is important to note that in this case, the two phytoplankton populations both dictate K which means that they can affect each other.

Final equations for the two phytoplantkon populations are now:

$$\frac{\partial \langle B_1 \rangle}{\partial t} = \frac{\alpha_1 I_0}{K z_m}\left(1 - e^{-K z_m}\right)\langle B_1 \rangle - L_1 \langle B_1 \rangle, \tag{5.20}$$

$$\frac{\partial \langle B_2 \rangle}{\partial t} = \frac{\alpha_2 I_0}{K z_m}\left(1 - e^{-K z_m}\right)\langle B_2 \rangle - L_2 \langle B_2 \rangle. \tag{5.21}$$

where $\langle B_1 \rangle$ and $\langle B_2 \rangle$ are defined as:

$$\int_0^{z_m} B_1 dz = \langle B_1 \rangle z_m, \tag{5.22}$$

$$\int_0^{z_m} B_2 dz = \langle B_2 \rangle z_m. \tag{5.23}$$

Numerical form of equations (5.20) and (5.21) is:

$$B_1(n+1) = B_1(n) + \frac{\alpha_1 I_0 \Delta t}{K z_m}\big(1 - e^{-K z_m}\big) B_1(n) - L_1 B_1(n)\Delta t, \tag{5.24}$$

$$B_2(n+1) = B_2(n) + \frac{\alpha_2 I_0 \Delta t}{K z_m}\big(1 - e^{-K z_m}\big) B_2(n) - L_2 B_2(n)\Delta t, \tag{5.25}$$

where Δt is the time step and n the time index.

We define A_1 and A_2 as the ratio of surface production to losses (uniform over depth):

$$A_1 = \frac{\alpha_1 I_0}{L_1}, \tag{5.26}$$

$$A_2 = \frac{\alpha_2 I_0}{L_2}. \tag{5.27}$$

Optically uncoupled critical depths C_1 and C_2 are the critical depths associated with $k_{B1} = 0$ and $k_{B2} = 0$ which are defined as [7]:

$$C_1 = \frac{1}{K_w}\Big(W_0(-A_1 e^{-A_1}) + A_1\Big), \tag{5.28}$$

$$C_2 = \frac{1}{K_w}\Big(W_0(-A_2 e^{-A_2}) + A_2\Big). \tag{5.29}$$

Optically coupled critical depths S_1 and S_2 are the critical depths associated with $k_{B1} \neq 0$ and $k_{B2} \neq 0$ which are defined as [7]:

$$S_1 = \frac{1}{K_w + k_{B1}B_1 + k_{B2}B_2}\Big(W_0(-A_1 e^{-A_1}) + A_1\Big), \tag{5.30}$$

$$S_2 = \frac{1}{K_w + k_{B1}B_1 + k_{B2}B_2}\Big(W_0(-A_2 e^{-A_2}) + A_2\Big). \tag{5.31}$$

Figures 7a and 7b show two different situations for optically coupled critical depths S_1 and S_2 for two phytoplankton populations.

Figure 6 shows two different situations of change of phyotplankton biomass over time for two phytoplankton populations. Figure 6a shows that phytoplantkon biomass $B_2(t)$ for the loosing species tends to zero (after a certain time this species dies out). Also, phytoplantkon biomass $B_1(t)$ for the wining species tends to a steady-state biomass B_1^*, regardless of initial conditions. It can be noticed at the begin of this simulation (first $1\ \mathrm{h}$) that magenta line decreases because of population 2 and blue line increases in that period.

Figure 6b shows that phytoplantkon biomass $B_1(t)$ for the loosing species tends to zero (after a certain time this species dies out). Also, phytoplantkon biomass $B_2(t)$ for the wining species tends to a steady-state biomass B_2^*, regardless of initial conditions. It can be noticed at the begining of this simulation (first $1\ \mathrm{h}$) that cyan line decreases because of population 1 and red line increases in that period, like in Figure 6a .

Steady state biomass of each species for this model are defined as:

$$B_1^* = \frac{K_w}{k_{B1}}\left(\frac{C_1}{z_m} - 1\right), \tag{5.32}$$

$$B_2^* = \frac{K_w}{k_{B2}}\left(\frac{C_2}{z_m} - 1\right). \tag{5.33}$$

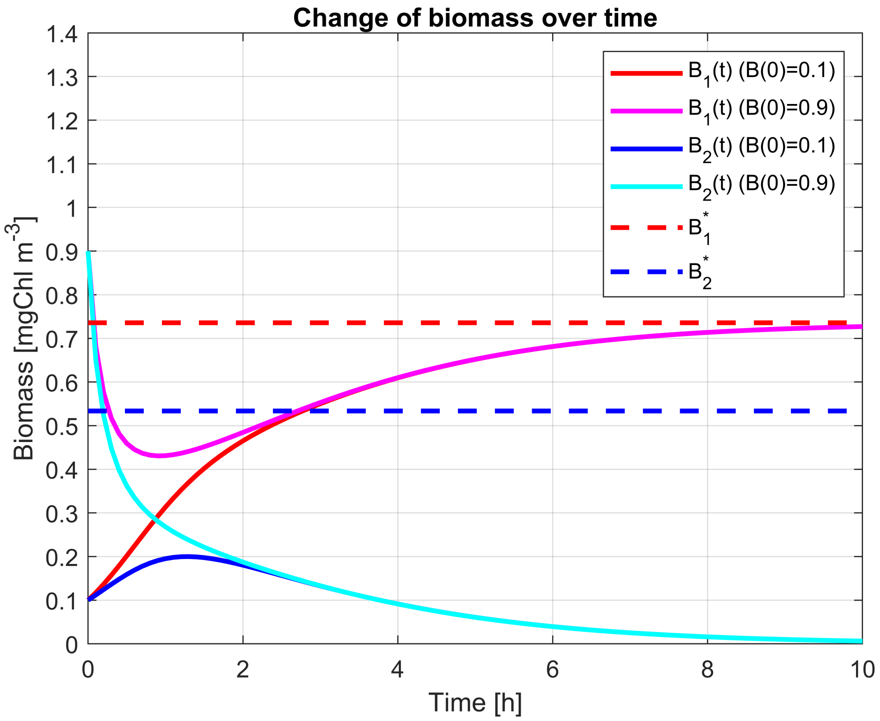
There are two cases for populations in this model:
a) The first case is when population 1 beats population 2, which means that the steady-state biomass value for population 2 is equal to zero:

$$B_2^* = 0. \tag{5.34}$$

b) The second case is when population 2 beats population 1, which means that the steady-state biomass value for population 1 is equal to zero:

$$B_1^* = 0. \tag{5.35}$$

(a) *Case when population 1 wins ($\alpha_1 = 0.22, \alpha_2 = 0.21$)*



(b) *Case when population 2 wins ($\alpha_1 = 0.21, \alpha_2 = 0.22$)*

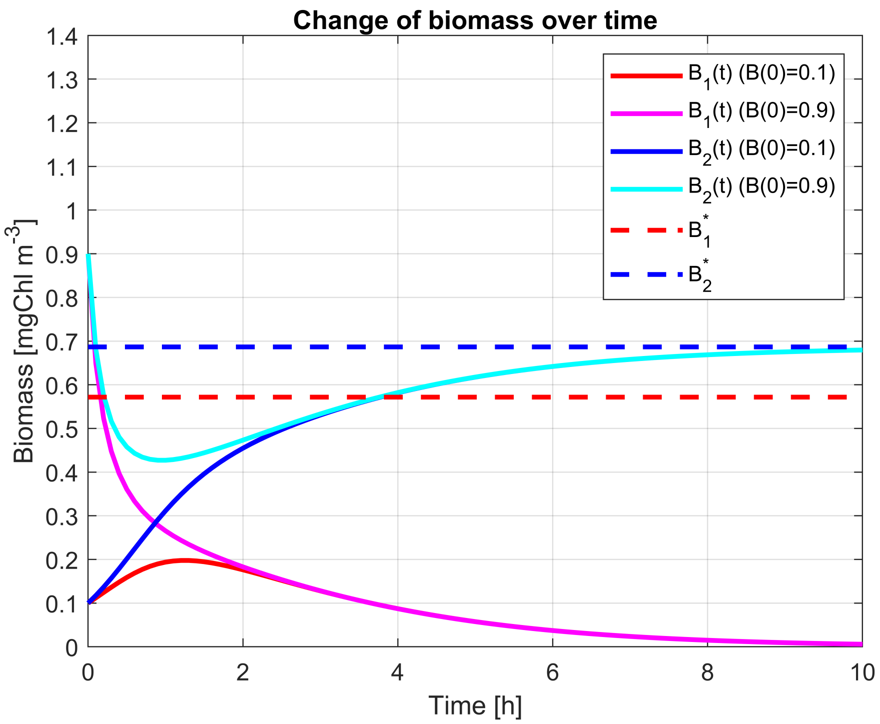


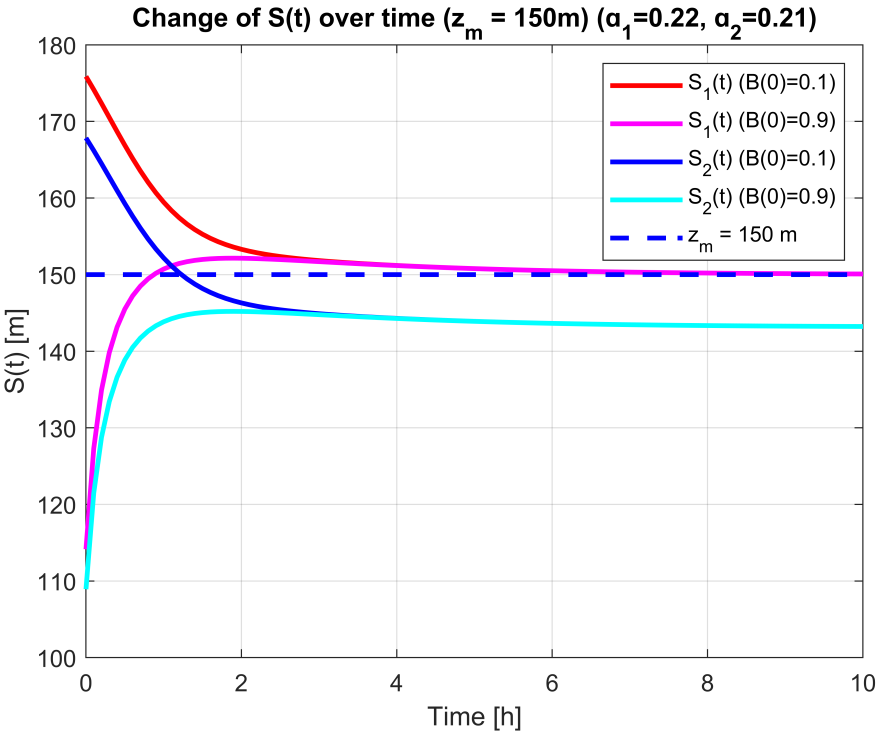
Figure 6: *Change of biomass B(t) over time in monochromatic model for two phytoplankton populations. Steady-state biomasses B_1^* and B_2^* are given with red and blue dashed line. Blue and cyan full line show phytoplankton biomass $B_1(t)$. Red and magenta full line show phytoplankton biomass $B_2(t)$. Different start points of lines correspond to different initial biomass conditions.*

Figure 7 shows two different situations of change of optically coupled critical depths $S_1(t)$ and $S_2(t)$ over time for monochromatic model with two phytoplankton populations. Red and blue line correspond to initial biomass of $0.1\ \mathrm{mgChl\,m^{-3}}$. Magenta and cyan line correspond to initial biomass of $0.9\ \mathrm{mgChl\,m^{-3}}$.

Figure 7a shows the case when population 2 wins. In this case initial slope for population 2 is greater than for population 1 ($\alpha_2 = 0.22\ \mathrm{mgC\,(mgChl)^{-1}\,W^{-1}\,m^{-2}\,h^{-1}}$, $\alpha_1 = 0.21$ $\mathrm{mgC\,(mgChl)^{-1}\,W^{-1}\,m^{-2}\,h^{-1}}$). Loss rate for each phytoplankton population has the same value $L_1 = L_2 = 10.2\ \mathrm{s^{-1}}$. Blue and cyan line, which show value of $S_2(t)$, over time tend to fixed value of mixed layer depth which is set at $z_m = 150$ m regardless of initial conditions. They tend to the same value regardless of initial conditions.

Figure 7b shows the case when population 1 wins. In this case the initial slope for population 1 is greater than for population 2 ($\alpha_1 = 0.22\ \mathrm{mgC\,(mgChl)^{-1}\,W^{-1}\,m^{-2}\,h^{-1}}$, $\alpha_2 = 0.21$ $\mathrm{mgC\,(mgChl)^{-1}\,W^{-1}\,m^{-2}\,h^{-1}}$). Loss rate for each phytoplankton population has the same value $L_1 = L_2 = 10.2\,\mathrm{s^{-1}}$. Red and magenta curve, which show value of $S_1(t)$, over time tend to fixed value of the mixed layer depth, which is set at $z_m = 150\ \mathrm{m}$. They tend to the same value regardless of initial conditions.

(a) *Case when population 1 wins* ($\alpha_1 = 0.22, \alpha_2 = 0.21$)



(b) *Case when population 2 wins* ($\alpha_1 = 0.21, \alpha_2 = 0.22$)

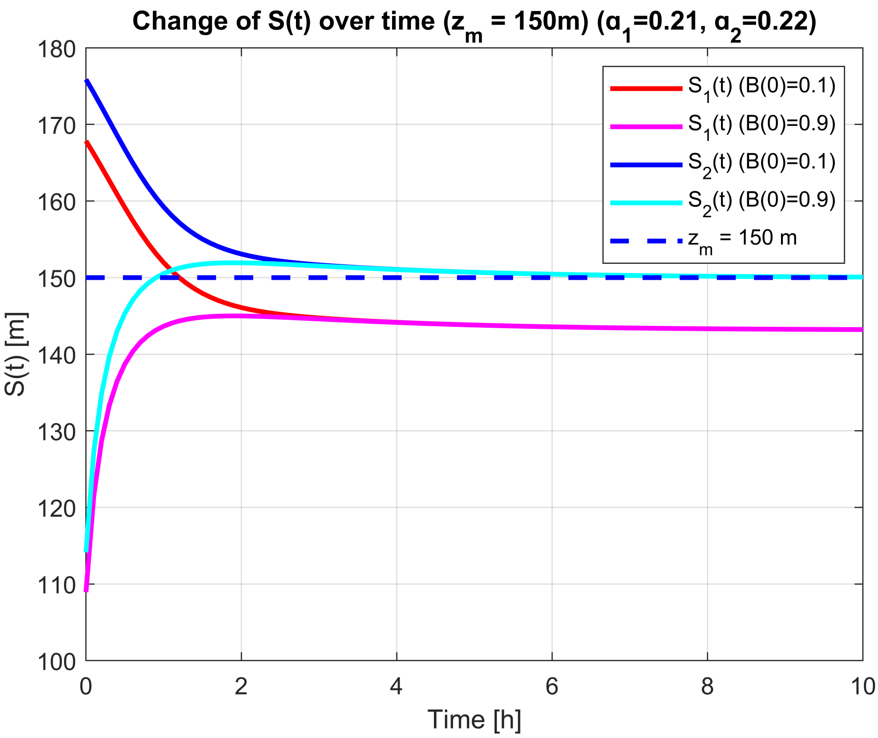


Figure 7: *Change of optically coupled critical depths* $S_1(t)$ *and* $S_2(t)$ *over time* t*. Blue dashed line shows the mixed layer depth* z_m*, red and magenta line show optically coupled critical depth* $S_1(t)$*, blue and cyan line show optically coupled critical depth* $S_2(t)$*. Different start points of lines correspond to different initial biomass conditions.*

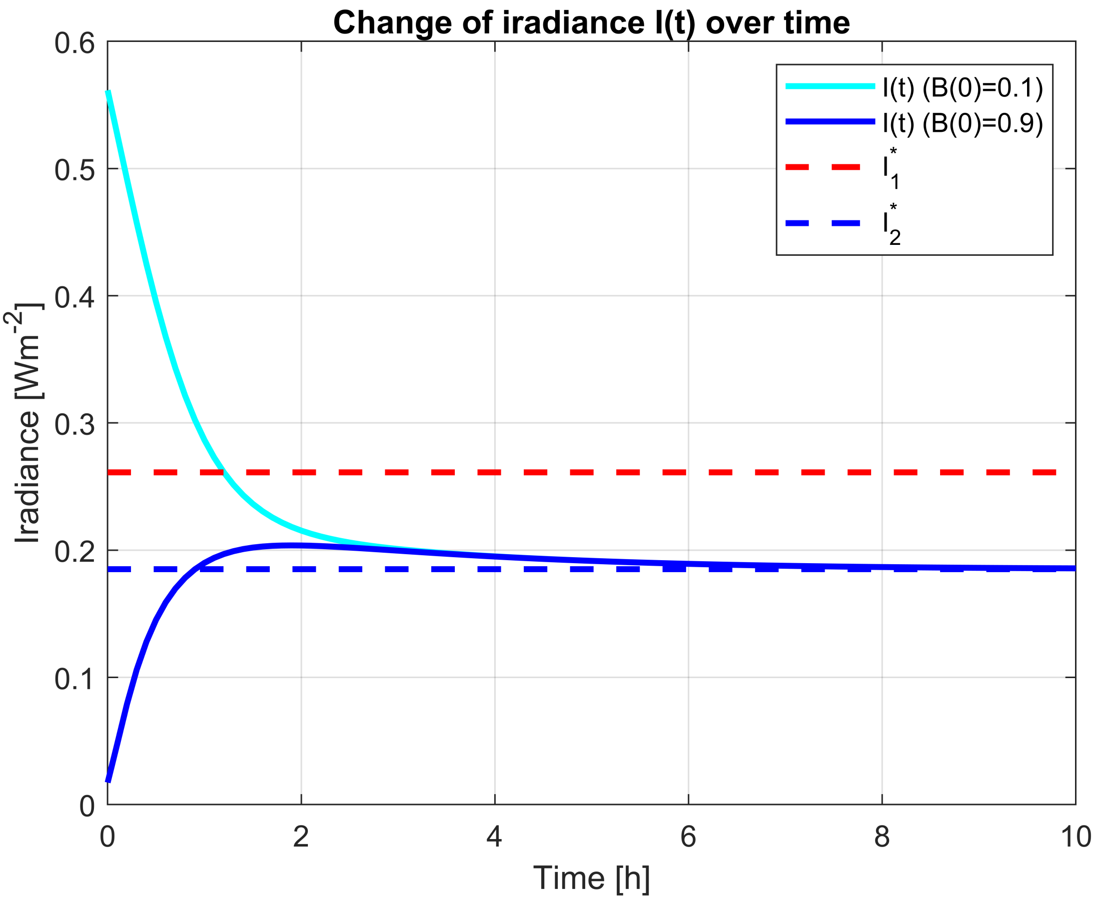


Figure 8: *Change of irradiance $I(t)$ over time t at mixed layer depth z_m. Red dashed line shows steady-state irradiance I_1^*, blue dashed line shows steady-state irradiance I_2^*, blue and cyan line show irradiance $I(t)$. Different start points of blue lines correspond to different initial biomass conditions.*

Using the equations (5.34) and (5.35) we can get two different values of steady-state irradiance depending on which population wins:

$$I_1^* = I_0 e^{-(K_w + k_{B1} B_1^*) z_m}, \tag{5.36}$$

$$I_2^* = I_0 e^{-(K_w + k_{B2} B_2^*) z_m}, \tag{5.37}$$

Figure 8 shows that irradiance $I(t)$, regardless of initial condition, tends to a steady-state irradiance I_2^* which is iradiance of the wining species in this case. Steady-state irradiance in this model is defined as:

$$I^* = I_0 e^{-(K_w + k_{B1} B_1^* + + k_{B2} B_2^*) z_m}. \tag{5.38}$$

Table 3: *Parameters used in a monochromatic model for two phytoplankton populations.*

Parameter	Amount	Unit
I_0	350	$\mathrm{W\,m^{-2}}$
L_1	10.1	$\mathrm{s^{-1}}$
L_2	10.2	$\mathrm{s^{-1}}$
z_m	150	m
α_1	0.21	$\mathrm{mgC\,(mgChl)^{-1}\,W^{-1}\,m^{-2}\,h^{-1}}$
α_2	0.22	$\mathrm{mgC\,(mgChl)^{-1}\,W^{-1}\,m^{-2}\,h^{-1}}$
K_W	0.04	$\mathrm{m^{-1}}$
k_{B1}	0.014	$\mathrm{m^2\,(mgChl)^{-1}}$
k_{B2}	0.015	$\mathrm{m^2\,(mgChl)^{-1}}$
B_0	(0.1 - 0.9)	$\mathrm{mgChl\,m^{-3}}$

5.3 Monochromatic model with N phytoplankton populations

The mathematical procedure for N phytoplankton populations is exactly the same as for one phytoplankton population. With N populations we have N advection-diffussion-reaction equations (5.1) for each population:

$$\frac{\partial B_i}{\partial t} + w\frac{\partial B_i}{\partial z} = D\frac{\partial^2 B_i}{\partial^2 z} + P_i - L_i B_i \quad \text{for} \quad i = 1, 2, ..., N, \tag{5.39}$$

where i is the index of each population. Primary production $P_i(z,t)$ for each population is now defined as:

$$P_i = \alpha_i I = \alpha_i I_0 e^{-Kz} \quad \text{for} \quad i = 1, 2, ..., N, \tag{5.40}$$

where α_i is initial slope for each population and K is atenuation coefficient which is now defined as:

$$K = K_w + \sum_{i=1}^{N}(k_{Bi}B_i). \tag{5.41}$$

Final equation for i-th biomass is:

$$\frac{\partial\langle B_i\rangle}{\partial t} = \frac{\alpha_i I_0\langle B_i\rangle}{Kz_m}\big(1 - e^{-Kz_m}\big) - L_i\langle B_i\rangle. \tag{5.42}$$

Numerical form of equation (5.42) is:

$$B_i(n+1) = B_i(n) + \frac{\alpha_i I_0 \Delta t}{Kz_m}\big(1 - e^{-Kz_m}\big)B_i(n) - L_i B_i(n)\Delta t. \tag{5.43}$$

We define A_i as the ratio of surface production to losses (uniform over depth):

$$A_i = \frac{\alpha_i I_0}{L_i}. \tag{5.44}$$

Optically uncoupled critical depth C_i is the critical depth associated with $k_{Bi} = 0$ and is defined as:

$$C_i = \frac{1}{K_w}\Big(W_0(-A_i e^{-A_i}) + A_i\Big). \tag{5.45}$$

Optically coupled critical depth S_i is the critical depth associated with $k_{Bi} \neq 0$ and is defined as:

$$S_i = \frac{1}{K_w + \sum_{i=1}^{N}(k_{Bi}B_i)}\Big(W_0(-A_i e^{-A_i}) + A_i\Big). \tag{5.46}$$

Table 4: *Parameters used in a monochromatic model for N phytoplankton populations (*i *is the population index in the range* $i = 1, 2, 3, ..., N$*).*

Parameter	Amount	Unit
I_0	350	$\mathrm{Wm^{-2}}$
L_i	10.1 + 0.1(i-1)	$\mathrm{s^{-1}}$
z_m	150	m
α_i	0.21 + 0.01(i-1)	$\mathrm{mgC(mgChl)^{-1}W^{-1}m^{-2}h^{-1}}$
K_W	0.04	$\mathrm{m^{-1}}$
k_{Bi}	0.014 + 0.001(i-1)	$\mathrm{m^2(mgChl)^{-1}}$
B_{0i}	0.5	$\mathrm{mgChl\,m^{-3}}$
N	5	-

Table 5: *Obtained values for cricital depth, steady-state biomass and steady-state irradiance in a monochromatic model for 10 phytoplankton populations.*

Critical depth C	Steady-state biomass B^*	Steady-state irradiance I^*
174.83	0.47	0.32
181.80	0.56	0.24
188.62	0.64	0.18
195.30	0.71	0.147
201.86	0.76	0.10
208.28	0.81	0.08
214.58	0.86	0.06
220.76	0.89	0.05
226.82	0.93	0.04
232.77	0.95	0.03

In table 5 we can see that the population which has the highest value of critical depth C and steady-state biomass B^* has the lowest value of steady-state irradiance I^*.

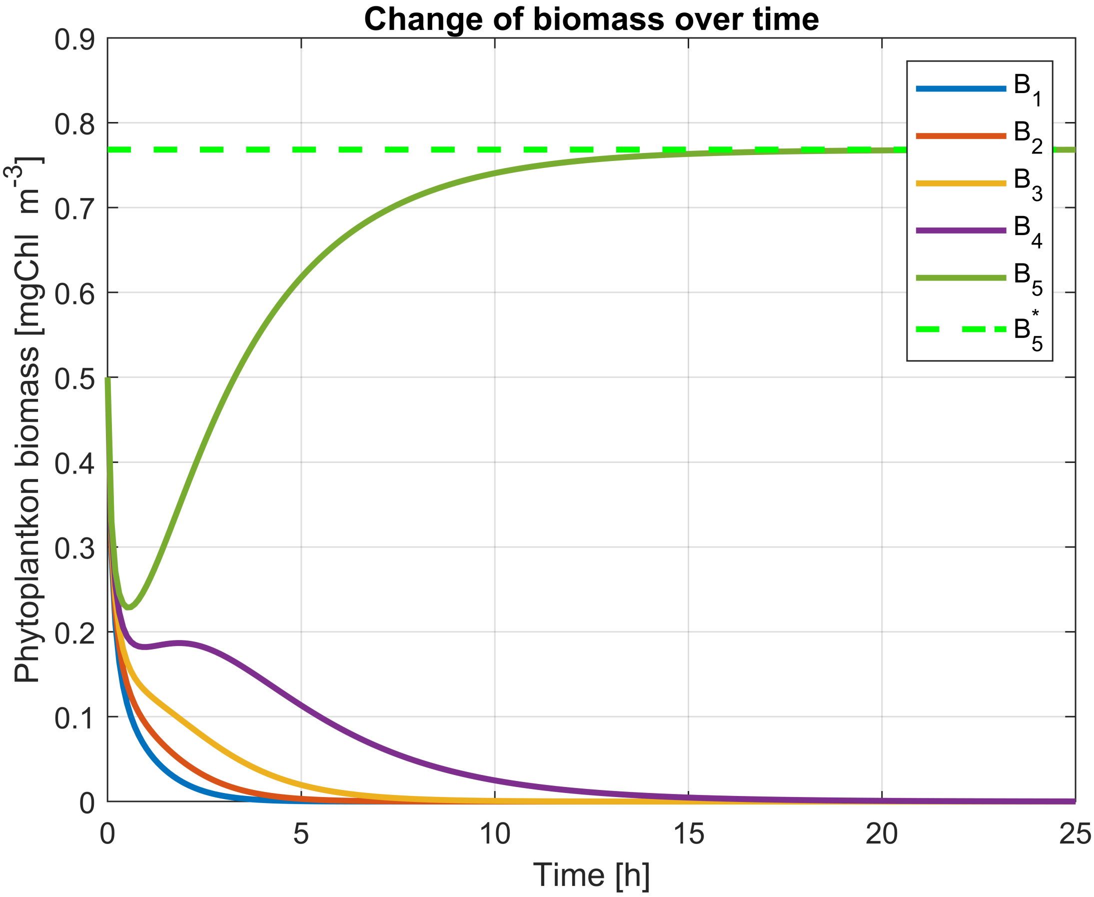


Figure 9: *Change of biomass B(t) over time in a monochromatic model for 5 phytoplankton populations. Phtoplankton biomasses B_1, B_2, B_3, B_4, B_5 are given with blue, red, orange, purple and green line. Steady-state biomass B_5^* is given with green dashed line.*

Figure 9 shows that biomass B_i of each loosing species (purple, orange, red and blue line) tends to zero. Phytoplantkon biomass $B_5(t)$ for the wining species (green line) tends to its steady-state biomass B_5^* (green dashed line). Only one population wins, regardless of initial conditions. At the begining of this simulation it can be seen that the biomass of the wining species (green full line) decreases then increases. The reason for this is that in the begining other species have a greater influence on K, until the victorious species overpower them. Steady-state biomass for this model is defined as:

$$B_i^* = \frac{K_w}{k_{Bi}}\left(\frac{C_i}{z_m} - 1\right), \quad \text{for} \quad i = 1, 2, ..., N. \tag{5.47}$$

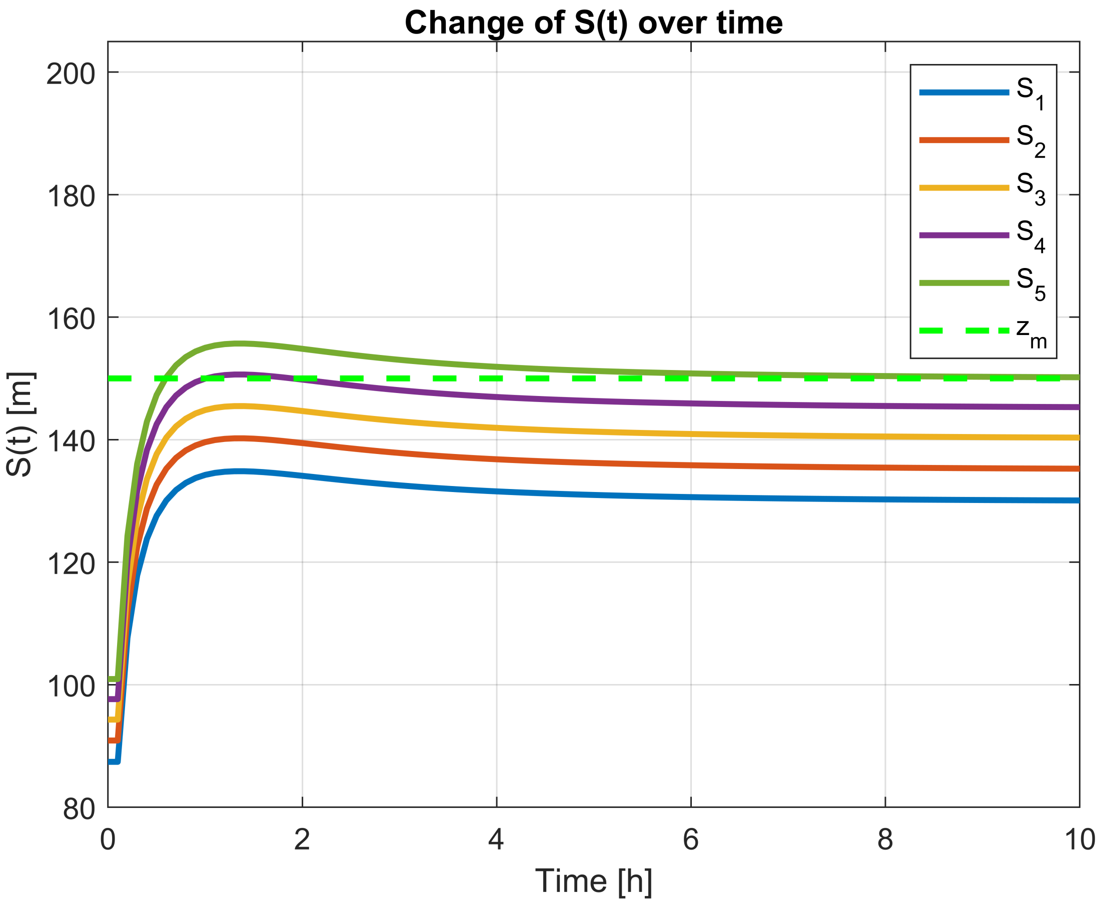


Figure 10: *Change of optically coupled critical depth S(t) over time in a monochromatic model for 5 phytoplankton populations. Optically coupled critical depths $S_i(t)$ for each phtoplankton population are described with different colours (blue for S_1, red for S_2, orange for S_3, purple for S_4 and green for S_5). Green dashed line stands for the mixed layer depth z_m.*

Figure 10 shows that optically coupled critical depths $S_i(t)$ for the loosing species (purple, orange, red and blue full line) do not converge to z_m. Optically coupled critical depth $S_i(t)$ (only one) for the wining species (green full line) tends to the mixed layer depth z_m (green dashed line). Inital biomass is $0.5\ \mathrm{mgChl\,m^{-3}}$. The wining species has the largest biomass B (only that species survives) and the depest optically coupled critical depth S.

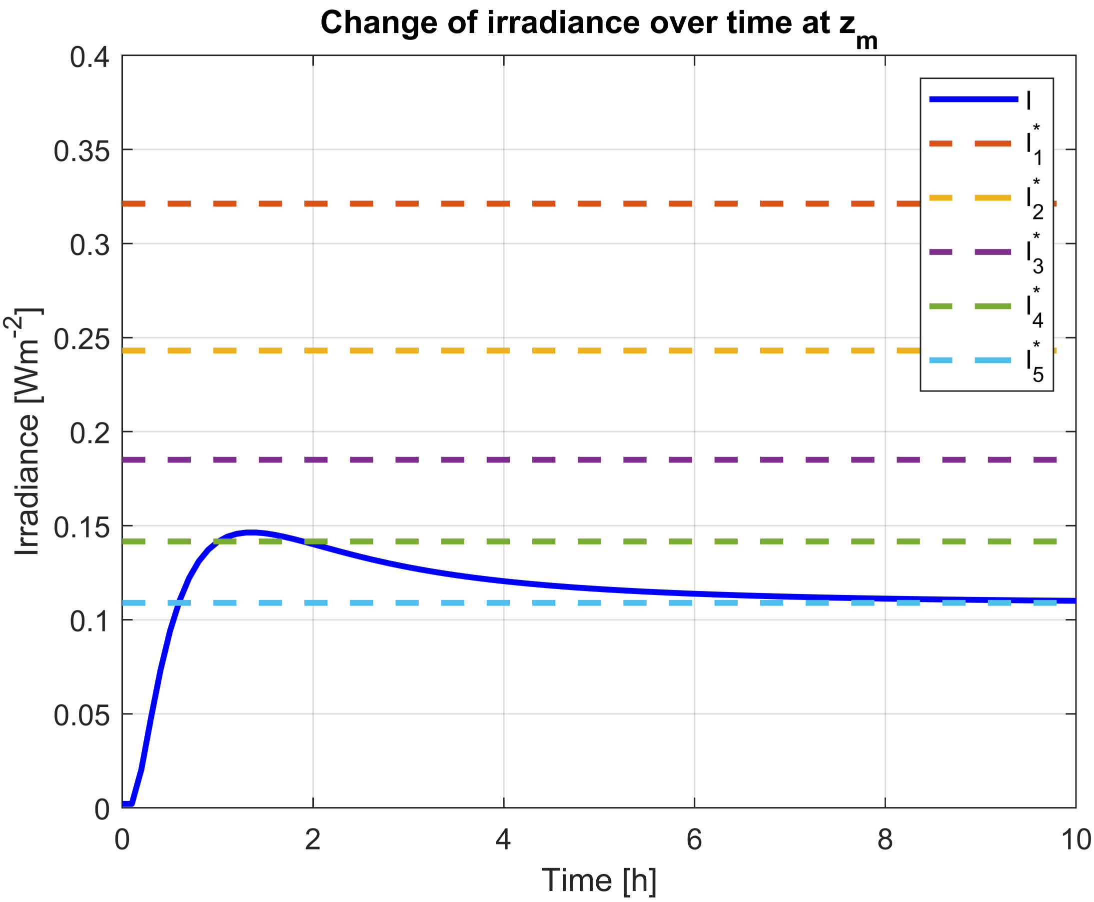


Figure 11: *Change of irradiance I(t) at the mixed layer depth z_m over time in a monochromatic model for 5 phytoplankton populations. Steady-state irradiance for each population is described with different dashed lines (red for I_1^*, orange for I_2^*, purple for I_3^*, green for I_4^* and cyan for I_5^*). Blue full line stands for irradiance $I(t)$.*

Figure 11 shows that irradiance $I(t)$ at the mixed layer depth z_m, regardless of initial conditions, tends to steady-state irradiance I_5^* which is equal to irradiance of the wining population 5 in this case. Steady-state irradiance in this model is defined as:

$$I^* = I_0 e^{-\left(K_w + \sum_{i=1}^{N} \left(k_{Bi} B_i^*\right)\right) z_m}. \tag{5.48}$$

We can get N different values of steady-state irradiance depending on which population wins:

$$I_i^* = I_0 e^{-(K_w + k_{Bi} B_i^*) z_m}, \quad \text{for} \quad i = 1, 2, ..., N \tag{5.49}$$

6 Spectral model

In this chapter the main idea is to observe the effect of spectrally resolved irradiances I_1 and I_2 on one and two phytoplankton populations.

6.1 Spectral model with one phytoplankton population

Irradiance is now split into 2 spectral bands I_1 and I_2:

$$I_1 = I_{01}e^{-K_1 z}, \tag{6.1}$$

$$I_2 = I_{02}e^{-K_2 z}, \tag{6.2}$$

where I_{01} and I_{02} represent surface irradiance of each spectral band and K_1 and K_2 are the atenuation coefficients which are now defined as:

$$K_1 = K_{w1} + k_1 B, \tag{6.3}$$

$$K_2 = K_{w2} + k_2 B, \tag{6.4}$$

where K_{w1} and K_{w2} are seawater attenuation coefficients, k_1 and k_2 are specific phytoplankton attenuation coefficients. Attenuation coefficients K_1 and K_2 give the rate of decrease of light intenstities I_1 and I_2 with depth.

We will once again use the advection-diffussion-reaction equation (5.1) to get the final equation for biomass:

$$\frac{\partial B}{\partial t} + w\frac{\partial B}{\partial z} = D\frac{\partial^2 B}{\partial^2 z} + PB - LB. \tag{6.5}$$

Primary production P is now defined as:

$$P = \alpha_1 I_1 + \alpha_2 I_2 = \alpha_1 I_{01}e^{-K_1 z} + \alpha_2 I_{02}e^{-K_2 z}, \tag{6.6}$$

where α_1 and α_2 are phytoplankton initial slopes which show the response (reaction) of phytoplankton to different light intensities I_1 and I_2. By including equations (6.3), (6.4) and (6.6) in equation (6.5) and integrating from the surface (0 m) to the mixed layer depth (z_m) we get:

$$\int_0^{z_m} \frac{\partial B}{\partial t}dz + \int_0^{z_m} w\frac{\partial B}{\partial z}dz = \int_0^{z_m} D\frac{\partial^2 B}{\partial^2 z}dz + \int_0^{z_m} \alpha_1 I_{01}e^{-K_1 z}B + \int_0^{z_m} \alpha_2 I_{02}e^{-K_2 z}B - \int_0^{z_m} LBdz. \tag{6.7}$$

After integration we get the following equation:

$$\frac{\partial \langle B\rangle}{\partial t}z_m + \left(wB - D\frac{\partial B}{\partial z}\right)\Big|_0^{z_m} = -\frac{\alpha_1 I_{01}}{K_1}e^{-K_1 z}\Big|_0^{z_m}\langle B\rangle - \frac{\alpha_2 I_{02}}{K_2}e^{-K_2 z}\Big|_0^{z_m}\langle B\rangle - L\langle B\rangle z_m, \tag{6.8}$$

where $\langle B \rangle$ is defined as:

$$\int_0^{z_m} B dz = \langle B \rangle z_m. \tag{6.9}$$

The fluxes on the surface (0) and the mixed layer depth (z_m) are assumed to be zero:

$$wB - D\frac{\partial B}{\partial z} = 0 \quad \text{for} \quad z = 0, \tag{6.10}$$

$$wB - D\frac{\partial B}{\partial z} = 0 \quad \text{for} \quad z = z_m. \tag{6.11}$$

By including these conditions and dividing equation (6.8) by z_m, the final equation for change of biomass over time is:

$$\frac{\partial \langle B \rangle}{\partial t} = \frac{\alpha_1 I_{01}}{K_1 z_m}\big(1 - e^{-K_1 z_m}\big)\langle B \rangle + \frac{\alpha_2 I_{02}}{K_2 z_m}\big(1 - e^{-K_2 z_m}\big)\langle B \rangle - L\langle B \rangle. \tag{6.12}$$

Now, the numerical form of equation (6.12) is:

$$B(n+1) = B(n) + \frac{\alpha_1 I_{01}\Delta t}{K_1 z_m}\big(1 - e^{-K_1 z_m}\big)B(n) + \frac{\alpha_2 I_{02}\Delta t}{K_2 z_m}\big(1 - e^{-K_2 z_m}\big)B(n) - LB(n)\Delta t, \tag{6.13}$$

where Δt is the time step and n the time index. We now simulate the temporal evolution of phytoplankton biomass B using equation (6.13). Table 6 contains all the parameter values used in this model.

Table 6: *Parameters used in the spectral model for one phytoplankton population.*

Parameter	Value	Unit
I_{01}	200	$\mathrm{W\,m^{-2}}$
I_{02}	150	$\mathrm{W\,m^{-2}}$
L	10	$\mathrm{s^{-1}}$
z_m	150	m
α_1	0.21	$\mathrm{mgC\,(mgChl)^{-1}W^{-1}\,m^{-2}\,h^{-1}}$
α_2	0.22	$\mathrm{mgC\,(mgChl)^{-1}W^{-1}\,m^{-2}\,h^{-1}}$
K_{w1}	0.041	$\mathrm{m^{-1}}$
K_{w2}	0.042	$\mathrm{m^{-1}}$
k_1	0.014	$\mathrm{m^2\,(mgChl)^{-1}}$
k_2	0.015	$\mathrm{m^2\,(mgChl)^{-1}}$
B_0	(0.1 - 0.9)	$\mathrm{mgChl\,m^{-3}}$

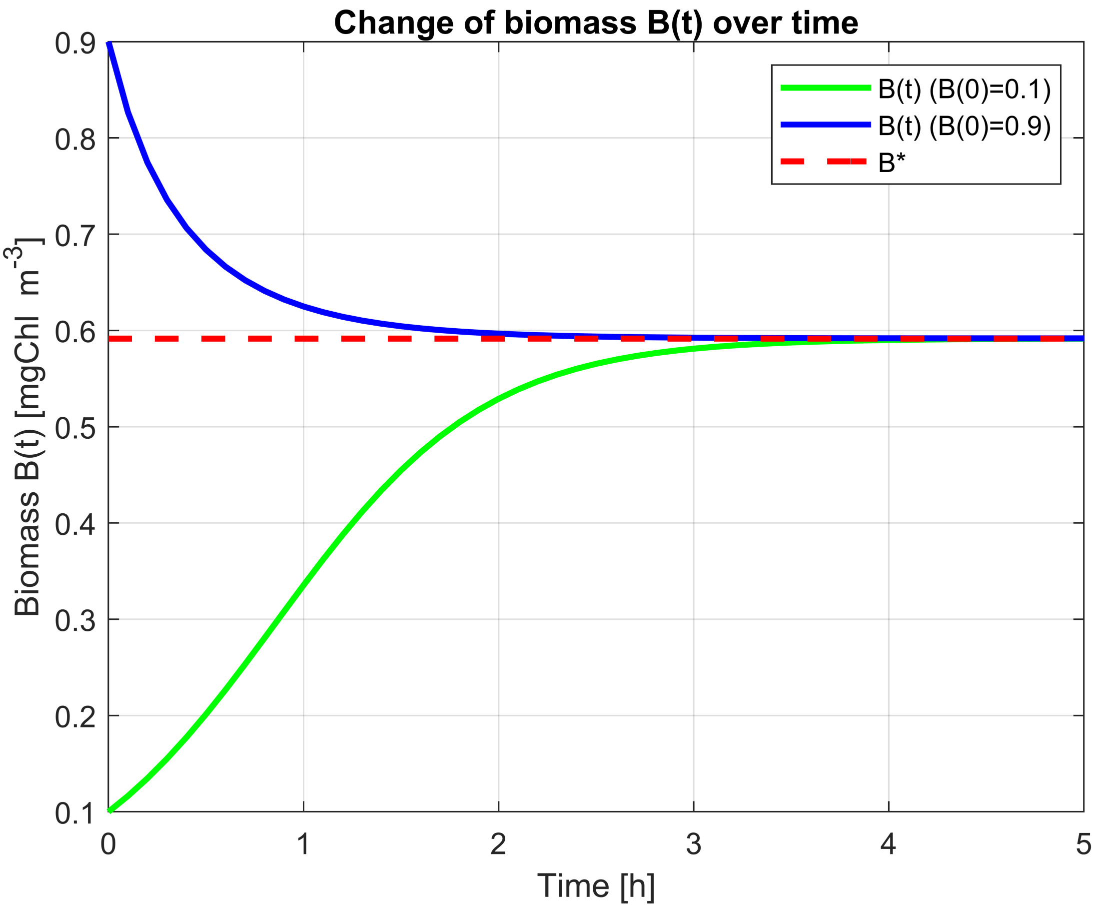


Figure 12: *Change of Biomass $B(t)$ over time in a spectral model with one phytoplankton population on the mixed layer depth z_m. Green line shows phtoplankton biomass B with initial condition of* $0.1\ \mathrm{mgChl\,m^{-3}}$*, blue line shows biomass B with initial condition of* $0.9\ \mathrm{mgChl\,m^{-3}}$ *and red dashed line shows steady-state biomass B^*.*

Figure 12 shows that biomass for one population with two spectral bands tends to a steady-state biomass (in this case steady-state biomass is at about $0.6\ \mathrm{mgChl\,m^{-3}}$). Biomass which is higher than steady-state biomass at the begining of the simulation decreases over time until it stabilizes. Biomass that is lower than steady-state biomass at the beginning of the simulation increases over time until it stabilizes. The duration of the simulation is 5 h which is sufficient to see the stabilization of the biomass.

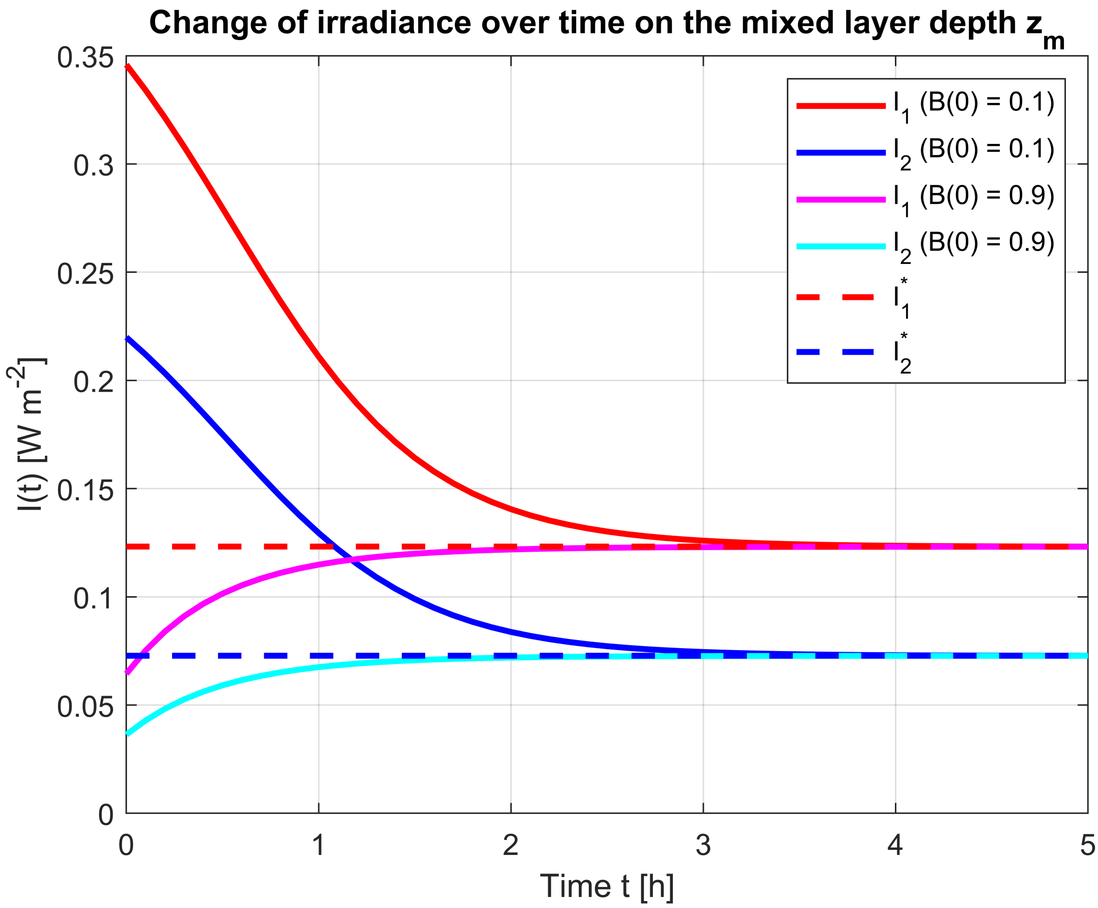


Figure 13: *Change of irradiance $I(t)$ over time at the mixed layer depth z_m in a spectral model with one phytoplankton population. Red and magenta line stand for a case when surface irradiance is 200 $\mathrm{W\,m^{-2}}$, blue and cyan line stand for a case when it is 150 $\mathrm{W\,m^{-2}}$. Different start points of lines correspond to different initial biomass conditions.*

Figure 13 shows change of two different irradiances over time at the mixed layer depth z_m. Red and magenta line corresponds to surface irradiance of $200\ \mathrm{W\,m^{-2}}$, while blue and cyan line shows the irradiance which corresponds to surface irradiance of $150\ \mathrm{W\,m^{-2}}$. The duration of the simulation is $5\ \mathrm{h}$ which is sufficient to see the stabilization of the irradiance. "Red" and "blue" irradiance correspond to initial conditions for biomass of $0.1\ \mathrm{mgChl\,m^{-3}}$. Red and magenta line tend to a steady-state irradiance I_1^*. "Blue" and "cyan" irradiance correspond to initial condition for biomass of $0.9\ \mathrm{mgChl\,m^{-3}}$. Blue and cyan line tend to a steady-state irradiance I_2^*. Curves that have irradiance on the begining of simulation greater than steady-state irradiance decrease over time. Curves that have irradiance on the begining of simulation smaller than steady-state irradiance increase over time.

6.2 Spectral model with two phytoplankton populations

We again use irradiance which is split into two spectral bands:

$$I_1 = I_{01}e^{-K_1 z}, \tag{6.14}$$

$$I_2 = I_{02}e^{-K_2 z}, \tag{6.15}$$

where I_{01} and I_{02} respresent surface irradiance of each spectral band and K_1 and K_2 are atenuation coefficients which are now defined as:

$$K_1 = K_{w1} + k_{11}B_1 + k_{12}B_2, \tag{6.16}$$

$$K_2 = K_{w2} + k_{21}B_1 + k_{22}B_2 \tag{6.17}$$

where K_{w1} and K_{w2} are seawater attenuation coefficients, B_1 and B_2 are phytoplankton biomass for each population, k_{11}, k_{12}, k_{21} and k_{22} are specific phytoplankton attenuation coefficients. Attenuation coefficients K_1 and K_2 give the rate of decrease of light intenstities I_1 and I_2 with depth.

We will once again use two advection-diffussion-reaction equations (5.1) to get the final equation for biomass of each population:

$$\frac{\partial B_1}{\partial t} + w\frac{\partial B_1}{\partial z} = D\frac{\partial^2 B_1}{\partial^2 z} + P_1 B_1 - L_1 B_1, \tag{6.18}$$

$$\frac{\partial B_2}{\partial t} + w\frac{\partial B_2}{\partial z} = D\frac{\partial^2 B_2}{\partial^2 z} + P_2 B_2 - L_2 B_2. \tag{6.19}$$

Primary production P_1 and P_2 for each population is now defined as:

$$P_1 = \alpha_{11}I_1 + \alpha_{12}I_2 = \alpha_{11}I_{01}e^{-K_1 z} + \alpha_{12}I_{02}e^{-K_2 z}, \tag{6.20}$$

$$P_2 = \alpha_{21}I_1 + \alpha_{22}I_2 = \alpha_{21}I_{01}e^{-K_1 z} + \alpha_{22}I_{02}e^{-K_2 z}, \tag{6.21}$$

where α_{11}, α_{12}, α_{21} and α_{22} are phytoplankton initial slopes which show the response (reaction) of phytoplankton photosynthesis rate of each population to different light intensities I_1 and I_2. By including equations (6.20) and (6.21) in equations (6.18) and (6.19) and integrating from the surface (0 m) to the depth of the mixed layer (z_m) we get:

$$\int_0^{z_m} \frac{\partial B_1}{\partial t}dz + \int_0^{z_m} w\frac{\partial B_1}{\partial z}dz = \int_0^{z_m} D\frac{\partial^2 B_1}{\partial^2 z}dz + \int_0^{z_m} P_1(z,t)dz - \int_0^{z_m} L_1 B_1 dz, \tag{6.22}$$

$$\int_0^{z_m} \frac{\partial B_2}{\partial t} dz + \int_0^{z_m} w\frac{\partial B_2}{\partial z} dz = \int_0^{z_m} D\frac{\partial^2 B_2}{\partial^2 z} dz + \int_0^{z_m} P_2(z,t) dz - \int_0^{z_m} L_2 B_2 dz. \tag{6.23}$$

By solving these integrals we get:

$$\frac{\partial\langle B_1\rangle}{\partial t} z_m + \left(wB - D\frac{\partial B_1}{\partial z}\right)\Bigg|_0^{z_m} = -\frac{\alpha_{11} I_{01}}{K_1} e^{-Kz}\Bigg|_0^{z_m} \langle B_1\rangle - \frac{\alpha_{12} I_{02} B_2}{K_2} e^{-Kz}\Bigg|_0^{z_m} \langle B_1\rangle - L_1\langle B_1\rangle z_m, \tag{6.24}$$

$$\frac{\partial\langle B_2\rangle}{\partial t} z_m + \left(wB - D\frac{\partial B_2}{\partial z}\right)\Bigg|_0^{z_m} = -\frac{\alpha_{21} I_{01}}{K_1} e^{-Kz}\Bigg|_0^{z_m} \langle B_2\rangle - \frac{\alpha_{22} I_{02}}{K_2} e^{-Kz}\Bigg|_0^{z_m} \langle B_2\rangle - L_2\langle B_2\rangle z_m, \tag{6.25}$$

where $\langle B_1\rangle$ and $\langle B_2\rangle$ are defined as:

$$\int_0^{z_m} B_1 dz = \langle B_1\rangle z_m, \tag{6.26}$$

$$\int_0^{z_m} B_2 dz = \langle B_2\rangle z_m. \tag{6.27}$$

The fluxes on the surface and the mixed layer depth are equal to zero:

$$wB_1 - D\frac{\partial B_1}{\partial z} = 0 \quad \text{for} \quad z = 0, \tag{6.28}$$

$$wB_1 - D\frac{\partial B_1}{\partial z} = 0 \quad \text{for} \quad z = z_m, \tag{6.29}$$

$$wB_2 - D\frac{\partial B_2}{\partial z} = 0 \quad \text{for} \quad z = 0, \tag{6.30}$$

$$wB_2 - D\frac{\partial B_2}{\partial z} = 0 \quad \text{for} \quad z = z_m. \tag{6.31}$$

By including these conditions and dividing equations (6.24) and (6.25) by z_m, the final equations are:

$$\frac{\partial\langle B_1\rangle}{\partial t} = \frac{\alpha_{11} I_{01}\langle B_1\rangle}{K_1 z_m}\left(1 - e^{-K_1 z_m}\right) + \frac{\alpha_{12} I_{02}\langle B_1\rangle}{K_2 z_m}\left(1 - e^{-K_2 z_m}\right) - L_1\langle B_1\rangle, \tag{6.32}$$

$$\frac{\partial\langle B_2\rangle}{\partial t} = \frac{\alpha_{21} I_{01}\langle B_2\rangle}{K_1 z_m}\left(1 - e^{-K_1 z_m}\right) + \frac{\alpha_{22} I_{02}\langle B_2\rangle}{K_2 z_m}\left(1 - e^{-K_2 z_m}\right) - L_1\langle B_2\rangle. \tag{6.33}$$

The numerical forms of these equations are:

$$B_1(n+1) = B_1(n) + \frac{\alpha_{11} I_{01} B_1(n)\Delta t}{K_1 z_m}\left(1 - e^{-K_1 z_m}\right) + \frac{\alpha_{12} I_{02} B_1(n)\Delta t}{K_2 z_m}\left(1 - e^{-K_2 z_m}\right) - L_1 B_1(n)\Delta t, \tag{6.34}$$

$$B_2(n+1) = B_2(n) + \frac{\alpha_{21} I_{01} B_2(n)\Delta t}{K_1 z_m}\left(1 - e^{-K_1 z_m}\right) + \frac{\alpha_{22} I_{02} B_2(n)\Delta t}{K_2 z_m}\left(1 - e^{-K_2 z_m}\right) - L_1 B_2(n)\Delta t, \tag{6.35}$$

where n is the time index and Δt is the time step. We now simulate the temporal evolution of phytoplankton biomass B using equations (6.32) and (6.33).

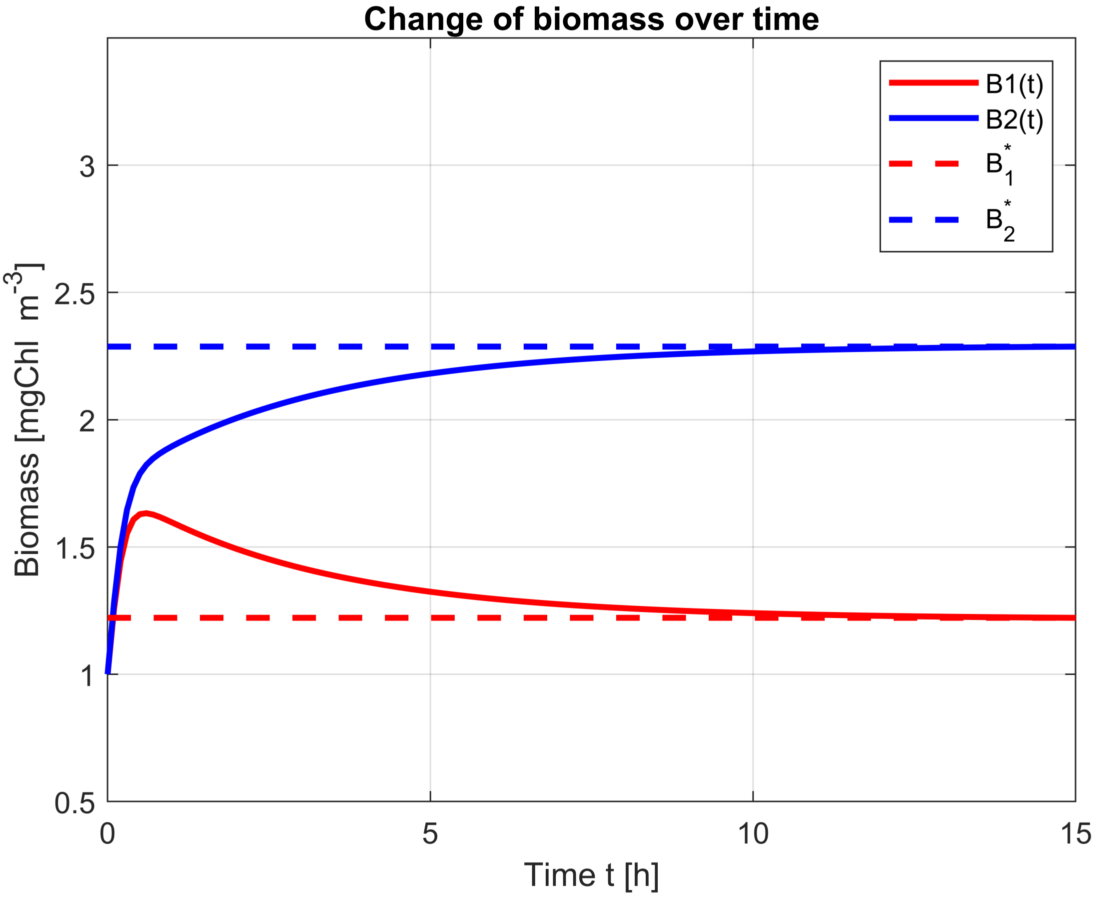


Figure 14: *Change of biomass B(t) on the mixed layer depth z_m in a spectral model with two phytoplankton population. Biomass B_1 is given with red line and biomass B_2 is given with blue line. Red dashed line shows steady-state biomass B_1^* and blue dashed line shows steady-state biomass B_2^*.*

Figure 14 shows phytoplankton biomass in a spectral model with two phytoplankton populations. Blue line shows phytoplankton biomass B_2 which has greater value of steady-state than biomass B_1 in this situation ($B_1^* < B_2^*$). Blue line tends to a steady-state biomass B_2^*. Red line shows phytoplankton biomass B_1 which has smaller value of steady-state biomass than B_2 in this situation ($B_1^* < B_2^*$). Red line tends to a steady state biomass B_1^*. The duration of the simulation is 15 h which is sufficient to see the stabilization of each biomass.

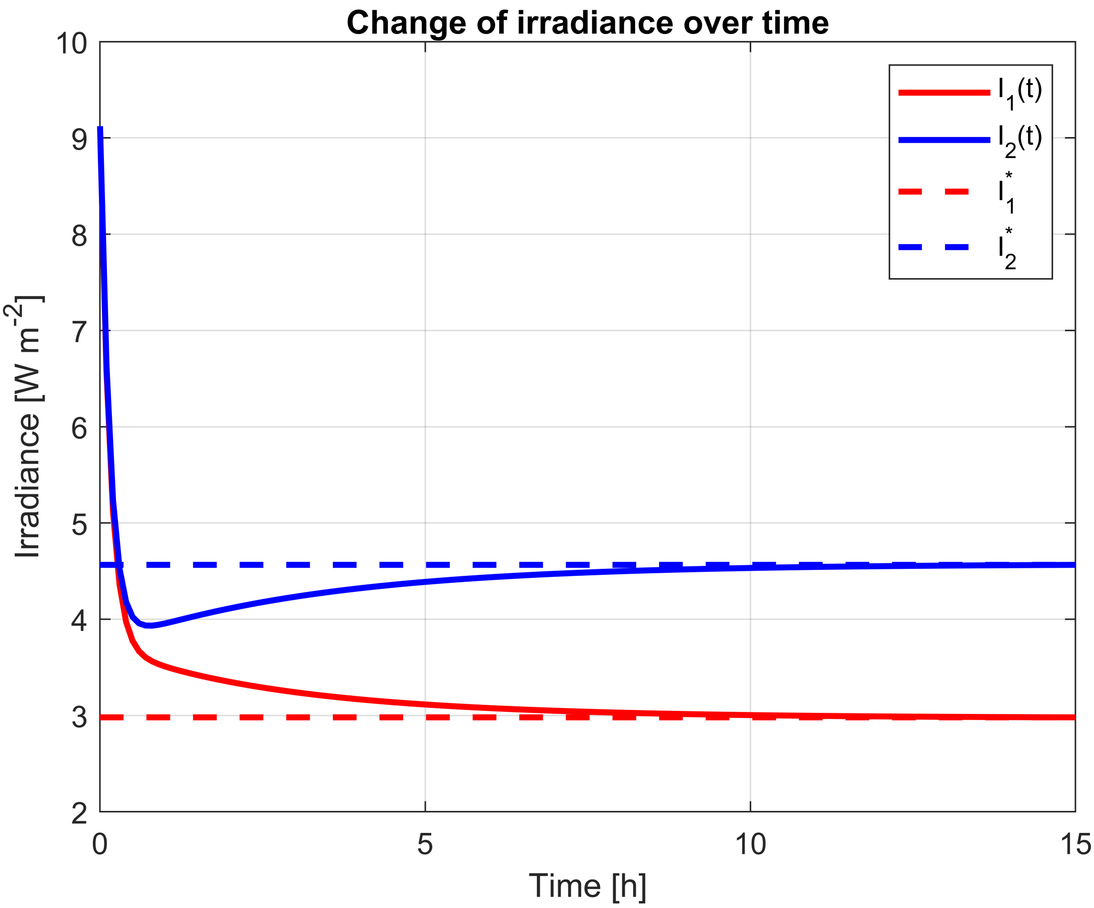


Figure 15: *Change of irradiances I_1 and I_2 over time in a spectral model with two phytoplankton populations at the mixed layer depth z_m. Red line corresponds to surface irradiance of $200\ \mathrm{Wm^{-2}}$, while blue line corresponds to surface irradiance of $150\ \mathrm{Wm^{-2}}$. Red dashed line shows steady-state irradiance I_1^*, blue dashed line shows steady-state irradiance I_2^*.*

Figure 15 shows change of two parts of irradiance over time at the mixed layer depth z_m in a spectral model with two phytoplankton populations. The duration of the simulation is $15\ \mathrm{h}$ which is sufficient to see the stabilization of the irradiance. Red line tends to a steady-state irradiance I_1^*. Blue line tends to a steady-state irradiance I_2^*. Initial biomass for both irradiance is $1\ \mathrm{mgChl\,m^{-3}}$. Table 6 contains all the parameter values used in this model in case when two phytoplankton populations survives.

Table 7: *Parameters used in a spectral model with two phytoplankton population in case when two populations survives (one example).*

Parameter	Value	Unit
I_{01}	200	$\mathrm{W\,m^{-2}}$
I_{02}	150	$\mathrm{W\,m^{-2}}$
L_1	10	$\mathrm{s^{-1}}$
L_2	10	$\mathrm{s^{-1}}$
z_m	150	m
α_{11}	0.1	$\mathrm{mgC\,(mgChl)^{-1}W^{-1}m^{-2}h^{-1}}$
α_{12}	0.15	$\mathrm{mgC\,(mgChl)^{-1}W^{-1}\,m^{-2}\,h^{-1}}$
α_{21}	0.15	$\mathrm{mgC\,(mgChl)^{-1}W^{-1}\,m^{-2}\,h^{-1}}$
α_{22}	0.105	$\mathrm{mgC\,(mgChl)^{-1}W^{-1}m^{-2}h^{-1}}$
K_{w1}	0.04	$\mathrm{m^{-1}}$
K_{w2}	0.04	$\mathrm{m^{-1}}$
k_{11}	0.05	$\mathrm{m^2\,(mgChl)^{-1}}$
k_{12}	0.02	$\mathrm{m^2\,(mgChl)^{-1}}$
k_{21}	0.02	$\mathrm{m^2\,(mgChl)^{-1}}$
k_{22}	0.05	$\mathrm{m^2\,(mgChl)^{-1}}$
B_{01}	(0.1 - 3)	$\mathrm{mgChl\,m^{-3}}$
B_{02}	(0.1 - 3)	$\mathrm{mgChl\,m^{-3}}$

7 Competition model for phytoplankton

The idea is to apply the analysis of the competition model in chapter 2 to our phytoplankton model. We will use equations of spectral model for two phytoplankton populations (6.32) and (6.33) and equalize them with zero to get stable states for each biomass:

$$\frac{\partial B_1}{\partial t} = \frac{\alpha_{11} I_{01} B_1}{K_1 z_m}\left(1 - e^{-K_1 z_m}\right) + \frac{\alpha_{12} I_{02} B_1}{K_2 z_m}\left(1 - e^{-K_2 z_m}\right) - L_1 B_1 = 0, \tag{7.1}$$

$$\frac{\partial B_2}{\partial t} = \frac{\alpha_{21} I_{01} B_2}{K_1 z_m}\left(1 - e^{-K_1 z_m}\right) + \frac{\alpha_{22} I_{02} B_2}{K_2 z_m}\left(1 - e^{-K_2 z_m}\right) - L_2 B_2 = 0. \tag{7.2}$$

Figure 16 shows the phase space of two phytoplankton biomass. In that space we can see "biomass flows". The arrows show us the flow or derivation of biomass (another example could be wind) that pushes points on the lines (in some places stronger, in some places weaker) to the end point. The different points from which the curves starts show different initial conditions. Regardless of the initial conditions, the curves always end at the same point, depending on the condition. If biomass B_1 wins then the curves end up on its axis and vice versa. In the case when both species survive, the curves will not end up on the any axes, but somewhere in the phase space.

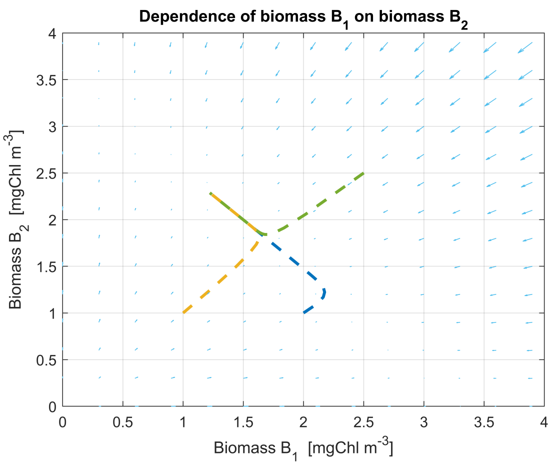
Figure 16a shows 3 lines (orange, blue and green) that take 3 different initial conditions for biomass at the beginning of the simulation. Orange line is corresponding to (B_{10}, B_{20}) = (1, 1), blue line is corresonding to (B_{10}, B_{20}) = (2, 1) and green line is corresponding to $(B_{10}, B_{20}) = (2.5, 2.5)$. All 3 lines end at the same point at $(B_1, B_2) = (1.22, 2.28)$. This point is closer to the y axis (B_2 axis) than the x axis (B_1 axis) on the graph, which mean that biomass B_2 has a higher steady-state value than biomass B_1 (population 2 has more than population 1). In this case, both populations survive on the end of simulation.

Figure 16b shows 3 lines that take 3 different initial conditions for biomass at the beginning of the simulation. Orange line is corresponding to $(B_{10}, B_{20}) = (1, 1)$, green line is corresponding to $(B_{10}, B_{20}) = (1, 2)$ and blue line is corresponding to $(B_{10}, B_{20}) = (2.5, 2.5)$. All 3 lines end at the same point at $(B_1, B_2) = (2.28, 1.22)$. This point is closer to the x axis (B_1 axis) than the y axis (B_2 axis) on the graph, which mean that biomass B_1 has a higher steady-state value than biomass B_2 (population 1 has more than population 2). In this case, both populations survive on the end of simulation.

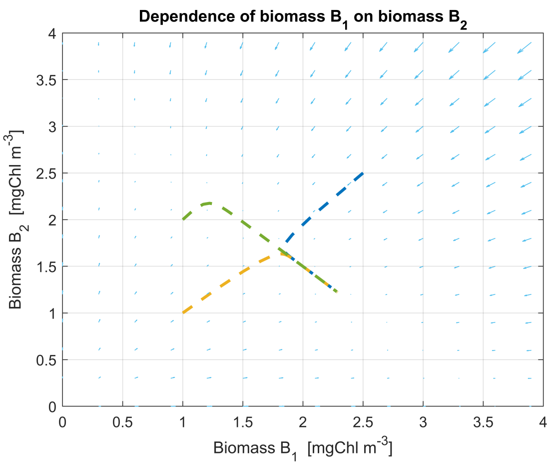
Figure 16c shows 3 lines that take 3 different initial conditions for biomass at the beginning of the simulation. Blue line is corresponding to $(B_{10}, B_{20}) = (1, 1)$, orange line is corresponding to $(B_{10}, B_{20}) = (2, 2)$ and green line is corresponding to $(B_{10}, B_{20}) = (2, 3)$. All 3 lines end at the same point at $(B_1, B_2) = (0, 5)$. This point is on the y axis (B_2 axis) on the graph, which mean that population with biomass B_2 is winner (steady-state value is not zero) and population with biomass B_1 is looser (steady-state is zero). In this case, population 2 at the end of simulation survives, while population 1 dies.

Figure 16d shows 3 lines corresponding to 3 different initial conditions for biomass at the beginning of the simulation. Blue line is corresponding to $(B_{10}, B_{20}) = (1, 2)$, orange line is corresponding to $(B_{10}, B_{20}) = (2, 3)$ and green line is corresponding to $(B_{10}, B_{20}) = (1, 1)$. All 3 lines end at the same point at $(B_1, B_2) = (3.82, 0)$. This point is on the x axis (B_1 axis) on the graph, which mean that population with biomass B_1 is winner (steady-state of biomass is not zero) and population with biomass B_2 is looser (steady-state of biomass is zero). In this case, population 1 at the end of simulation survives, while population 2 dies.

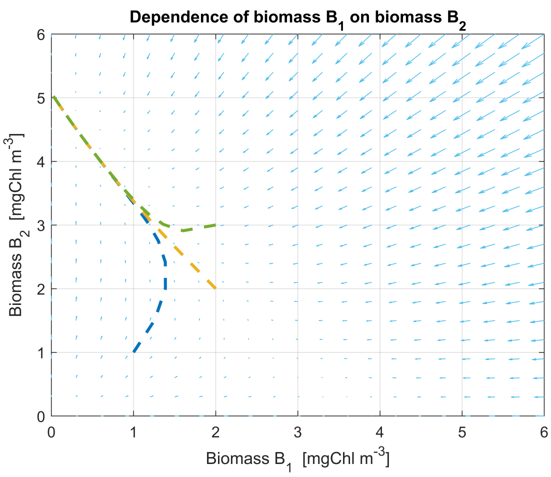
(a) *Case when* $\alpha_{12} = \alpha_{21} = 0.15$, $\alpha_{11} = 0.1$ *and* $\alpha_{22} = 0.105$



(b) *Case when* $\alpha_{12} = \alpha_{21} = 0.15$ *and* $\alpha_{11} = 0.105$ *and* $\alpha_{22} = 0.1$



(c) *Case when* $\alpha_{11} = \alpha_{21} = 0.15$, $\alpha_{22} = 0.15$ *and* $\alpha_{12} = 0.1$.



(d) *Case when* $\alpha_{11} = 0.15$, $\alpha_{12} = 0.1$ *and* $\alpha_{21} = \alpha_{22} = 0.105$

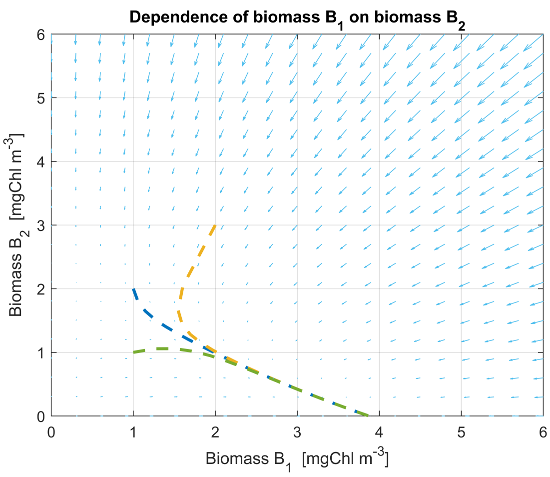
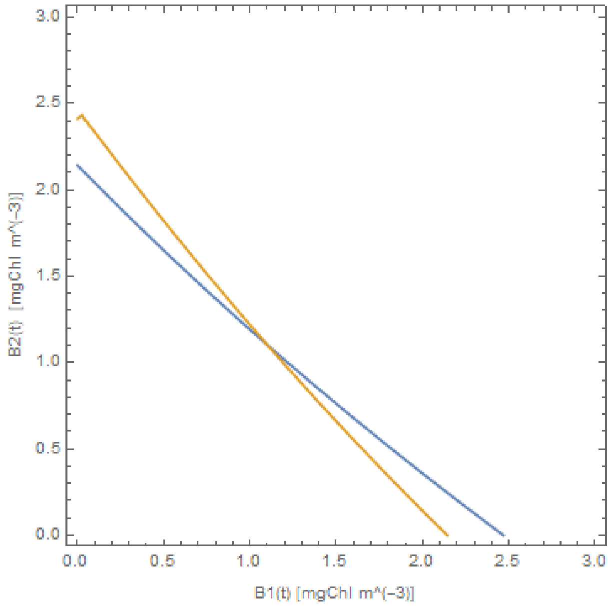


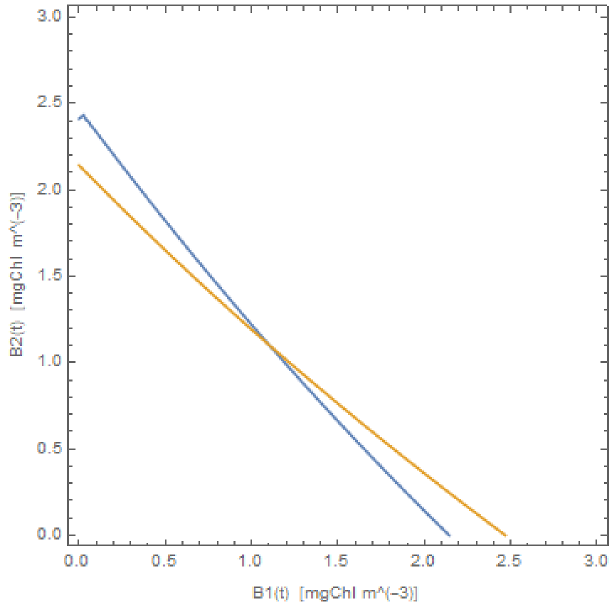
Figure 16: *The phase space of two phytoplankton biomass* $B_1(t)$ *and* $B_2(t)$ *in a spectral model with two phytoplankton populations. The arrows on the figures show biomass flows that actually push certain points in a certain direction. The different points from which the curves (green, orange and blue) starts show different initial conditions for biomass.*

Figure 17 shows null clines of phytoplankton biomass for various cases of α_{11}, α_{12}, α_{21} and α_{22} . In case the curves intersect, both species can survive. In the case when one curve is above the other, it means that the biomass corresponding to curve above has won the competition and has beaten the one below. It can be noticed that these curves look quite similar to the curves in Chapter 2 where we talked about the competititon model in general.

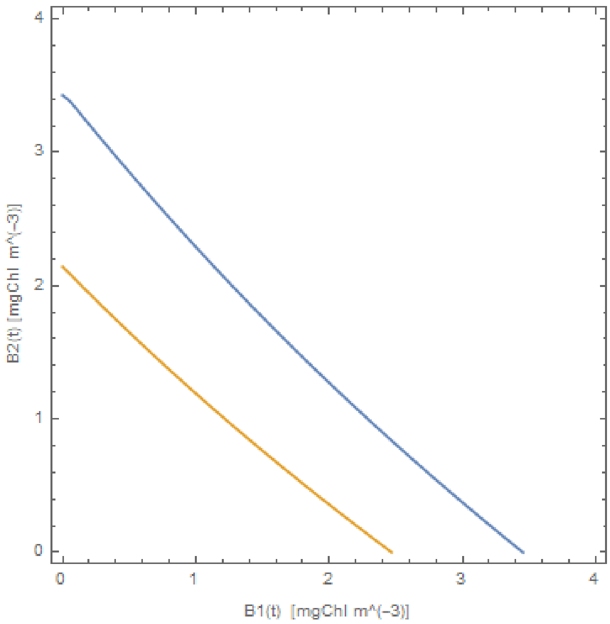
(a) *Case when* $\alpha_{11} = \alpha_{22} = 0.15$ *and* $\alpha_{12} = \alpha_{21} = 0.1$



(b) *Case when* $\alpha_{11} = \alpha_{22} = 0.1$ *and* $\alpha_{12} = \alpha_{21} = 0.15$



(c) *Case when* $\alpha_{11} = \alpha_{12} = \alpha_{21} = 0.15$ *and* $\alpha_{22} = 0.1$



(d) *Case when* $\alpha_{22} = \alpha_{12} = \alpha_{21} = 0.15$ *and* $\alpha_{11} = 0.1$

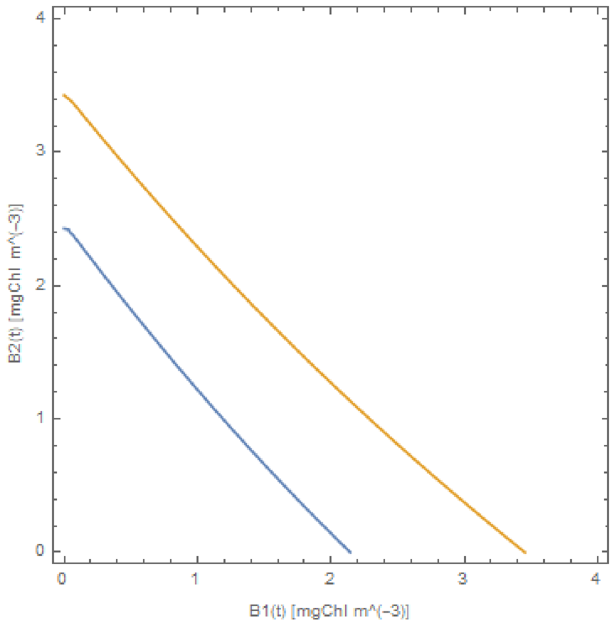


Figure 17: *Shematic phase trajectories for the various cases of* α_{11}, α_{12}, α_{21} *and* α_{22}. *Blue curve stands for equation* (7.1) , *orange curve stands for equation* (7.2).

8 Conclusion

At the beginning of this work a basic competition model, that shows competition of different species for same resource, is described. Figure 1 shows different outcomes of competition for two species. The idea in this work was to apply this competition model way of thinking to Sverdrup's model of critical depth, which describes the necessary conditions for phytoplankton survival in the ocean. In order to calculate the expression for the change of biomass over time, the problem was formulated as a typical advection-diffusion-reaction model and was integrated over depth for each type of phytoplakton. Initially, we explored how light intensity affects one species of phytoplankton. For this case, Figure 4 and 5 show the change in biomass and light intensity over time. Further in the paper, the same effect of light intensity was observed for two and more phytoplankton species. Graphs were obtained for biomass in which it can be seen that of the N phytoplantkon populations only one can win. The winner is the phytoplankton population that needs the least light.

In the second part of this work, we observed the effect of spectrally resolved light on one and two phytoplankton populations. For two phytoplantkon populations we observed that in certain situations both species can survive. Further in the work, we applied the general competition model to a specific case of phytoplankton. Using different equations ((2.4), (2.5), (7.1) and (7.2)) in the general and specific (phytoplankton) competition model, very similar graphs for different situations were obtained (Figure 1 and 17). Also, at the end of the work, Figure 16 is obtained which shows the phase space of two different phytoplankton types in which arrows represent biomass flows. These flows are actually derivatives of biomass over time that "push" the starting points on the graphs to some end points. The starting points of the curves represent different initial conditions, while the ending points depict which species wins the competition.

This work is a continuation of the well-known theory of the part of physical oceanography related to phytoplankton and spring blooms. In this work the competition model, critical depth theory and a primary production model are connected with a monochromatic and a spectral model for phytoplankton. This theory has been experimentally confirmed which is mentioned in [11] and other works. Many works mentioned in the literature are connected with this topic. This work shows that competition model works well. This topic could be extended to look at a richer light spectrum on the surface and more populations, which would further complicate the mathematical derivation and the final equations obtained. Also, we could take different forms of light intensity and in that way look at what kind of graphs and results we will get.

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A Appendix - codes

This chapter presents codes used in this thesis that were needed to obtain graphs for different situations. MATLAB R2020b and Wolfram Mathematica 11.1 programs were used for coding. In program MATLAB R2020b codes were made for monochromatic model with one, two and N phytoplankton populations and the spectral model with one and two phytoplankton populations. In program Wolfram Mathematica 11. codes were made for the competition model from the literature [4] and competition model applied for phytoplankton.

```
%-----Monochromatic model with one phytoplankton population-------

%Cleaning memory:
clear; clc; clear vars;

%Used constants:
I0 = 350;
Kw = 0.04;
k1 = 0.014;
alfa = 0.2;
L = 10;
zm = 150; %Mixed layer depth [m]

dt = 0.1;
T = 10;
t =  (0 : dt : T)';

A = alfa * I0 / L;

%Initial conditions:
%B(1,1) = (0.9).*rand(1,1);
B(1,1) = 0.1;
S (1,1) = ( 1 / (Kw + k1*B(1,1)) ) * (  lambertw(-A *exp(-A))  + A  );
I (1,1) = I0 * exp(- (Kw + k1*B(1,1)) * zm );

for  n = 1 : length(t) - 1

K1 = Kw + k1*B(n,1);
B (n+1,1)=B(n,1)+B(n,1)*(((alfa* I0 ) / (K1*zm))*(1-exp (-K1*zm))-L)*dt ;
S (n+1,1) = (  1 / (Kw + k1*B(n+1,1))    ) * ( lambertw(-A*exp(-A)) + A);
I (n+1,1) = I0 * exp(- (Kw + k1*B(n+1,1)) * zm );

end

C = (1 / Kw) * ( lambertw(-A*exp(-A)) + A );
Bz = (Kw / k1) * (C / zm - 1);
Iz  = I0 * exp(- (Kw + k1*Bz) * zm );
```

```
figure
plot(t , B (:, 1),  'b' , 'LineWidth', 1)
hold on
plot (t, Bz*ones(size(B (:, 1))) , '--g' , 'LineWidth'  , 2)
xlim([0 5])
title ("Change in biomass over time")
ylabel("Phytoplankton biomass [mmol m^{-3}]")
xlabel("Time [h]")
grid on
hold on
legend ('B_0=0.1' , 'B^*')

figure
plot(t , S (:, 1),  'b' , 'LineWidth', 1)
hold on
plot (t, zm*ones(size(S (:, 1))) , '--b' , 'LineWidth', 2)
xlim([0 8])
title ("Change in function S(t) over time")
ylabel("S(t)")
xlabel("Time [h]")
grid on
hold on
legend ('S(B_0=0.1)' , 'zm')

figure
plot(t , I (:, 1),  'b' , 'LineWidth', 1)
hold on
hold on
plot (t, Iz*ones(size(I (:, 1))) , '--r' , 'LineWidth', 2)
title ("Change in irradiance over time")
ylabel("Irradiance I(t) [W/m^2]")
xlabel("Time [h]")
grid on
hold on
legend ('I(B_0=0.1)' , 'I^*')
```

```
%-------Monochromatic model with two phytoplankton population---------
%Used constants:
I0 = 350;  %[W/m^2]
Kw = 0.04;
K1 = 0.014;
K2 = 0.015;
alfa1 = 0.21;
alfa2 = 0.21;
L1 = 10.1;
L2 = 10.2;
zm = 150; %mixed layer depth [m]
dt = 0.1;
T = 30;
t =  (0 : dt : T)';

A1 = alfa1 * I0 / L1;
A2 = alfa2 * I0 / L2;

%Initial conditions:
B1(1,1) = 0.5.*rand(1,1);
B2(1,1) = B1(1,1);
I (1,1) = I0 * exp(- (Kw + K1*B1(1,1) + Kw + K2*B2(1,1)  ) * zm );
S1 (1,1) =(1 / (Kw+K1*B1(1,1)+K2*B2(1,1)))*(lambertw(-A1 *exp(-A1))+A1);
S2 (1,1) =(1 / (Kw +  K1*B1(1,1) + K2*B2(1,1)) )*( lambertw(-A2 *exp(-A2)) + A2);

for  n = 1 : length(t) - 1
K = Kw + K1*B1(n,1) + K2*B2(n,1);
B1 (n+1,1)=B1(n,1)+B1(n,1)*(((alfa1* I0)/(K*zm))*(1 - exp (-K*zm))-L1) *dt;
B2 (n+1,1)=B2(n,1)+B2(n,1)*(((alfa2* I0)/(K*zm))*(1 - exp (-K*zm))-L2) *dt;
S1(n+1,1)=(1 / ( Kw + K1*B1(n+1,1)   + K2*B2(n+1,1) )) * ( lambertw(-A1*exp(-
A1)) + A1);
S2 (n+1,1) = (1 / ( Kw + K1*B1(n+1,1)  + K2*B2(n+1,1) ) ) *( lambertw(-A2*exp(-
A2))+A2);
I (n+1,1) = I0 * exp(- (Kw +    K1*B1(n+1,1)  + K2*B2(n+1,1) )   * zm );
end

C1 = (1 / Kw) * ( lambertw(-A1*exp(-A1)) + A1 );
C2 = (1 / Kw) * ( lambertw(-A2*exp(-A2)) + A2 );
Bz1 = (Kw / K1) * (C1 / zm - 1);
Bz2 = (Kw / K2) * (C2 / zm - 1);
```

```
Iz1  = I0 * exp(- (Kw + K1*Bz1) * zm );
Iz2  = I0 * exp(- (Kw + K2*Bz2) * zm );
Iz =  I0 * exp(- (Kw + K1*Bz1 + K2*Bz2) * zm );

figure
plot(t  , B1, 'g' , 'LineWidth' , 2)
hold on
plot(t  , B2, 'b' , 'LineWidth', 2)
plot (t, Bz1*ones(size(B1)) , '--g' ,  'LineWidth', 2 )
plot (t, Bz2*ones(size(B2)) , '--b' , 'LineWidth', 2)
title ("Changing of biomass over time")
ylabel("Biomass [mmol m^{-3}]")
xlabel("Time [h]")
grid on
legend('B_1(t)', 'B_2(t)', 'B^*_1' , 'B^*_2')

figure
plot (t, I , 'b', 'LineWidth', 1)
hold on
plot (t, Iz1*ones(size(I)) , 'g' , 'LineWidth', 2)
plot (t, Iz2*ones(size(I)) , 'r', 'LineWidth',  2)
title ("Change of iradiance I(t) over time")
ylabel("Iradiance [W/m^2]")
xlabel("Time [h]")
grid on
legend('I(t)' , 'I^*_1' , 'I^*_2')

figure
plot(t , S1, 'g' , 'LineWidth', 1)
hold on
plot(t , S2, 'b' , 'LineWidth', 1)
plot (t, C1*ones(size(S1)) , 'g' , 'LineWidth', 1 )
plot (t, C2*ones(size(S2)) , 'b' , 'LineWidth', 1)
plot (t, zm*ones(size(S2)) , 'r', 'LineWidth' , 2)
title ("Change of S(t) over time (z_m = 150m)")
ylabel("S(t)")
xlabel("Time [h]")
grid on
legend('S_1(t)','S_2(t)', 'z_m = 150 m')
```

```
%-----Monochromatic model with N phytoplankton population-------

%Cleaning memory:
clear; clc; clear vars;

dt = 0.1;  %1h [s]
T = 10;
t =  (0 : dt : T)';

%Used constants:
zm = 150; %mixed layer depth [m]
I0 = 350;  %[W/m^2]
Kw = 0.04;
N = 10; %number of populations (species)

%Matrix:
B (length(t), N) = zeros;
S (length(t), N) = zeros;
I  (length(t), N) = zeros;
K (length(t), 1) = zeros;
A (1, N) = zeros;
alfa (1, N) = zeros;
L (1, N) = zeros;
Kb (N, 1) = zeros;

%Initial conditions:
for i = 1:N
    Kb  (1, i) = 0.014 + 0.001*(i-1);
    alfa (1, i) = 0.2 + 0.01*(i-1);
    L (1, i) =     10 + 0.1*(i-1);
    B (1, i) = 0.5;
end

KB = 0;

%Initial conditions:
for i = 1: N
    KB = KB + Kb(1, i)*B(1, i);
end
```

```
for i = 1: N
    K (1, 1) = Kw + KB;
    I  (1, i) = I0 * exp( - ( K(1, 1) ) * zm );
    A (1, i) = alfa (1,i) * I0 / L(1, i);
    S (1, i) = (  1 / ( K(1, 1) )   ) * (  lambertw(-A(1,i) *exp(-A(1, i)))   + A(1, i));
end

 for  n = 1 : length(t) - 1
        for i = 1: N
                KB = 0;
                for k = 1:N
                            KB = KB + Kb(1, k)*B(n, k);
                end
                K (n, 1) = Kw + KB;
B (n+1, i) = B(n, i) + B(n, i) *(( (alfa (1, i) * I0 ) / (K (n, 1) *zm))*(1 - exp(-K(n,1)
*zm ) )  -  L(1, i) ) * dt  ;

  S (n+1, i) = (   1 / (  K(n, 1) )    ) * ( lambertw( -A (1, i) *exp(-A (1, i)) )   + A (1, i));
                I (n+1, i) =  I0 * exp(  - ( K(n, 1)  )* zm  ) ;
        end
end

Iz (1,N)  = zeros;
Bz (1,N) = zeros;
C (1,N) = zeros;
matrica (N, 3) = zeros; %(i,j)

for i = 1: N
    C  (1, i) = (1 / Kw) * ( lambertw( -A(1, i)*exp(-A(1, i))  )  + A(1, i) );
    Bz (1, i) = ( Kw / Kb(1, i) ) * ( (C (1,i) / zm) - 1);
    Iz  (1, i)  = I0 * exp(- ( Kw + Kb(1, i)*Bz(1, i)  ) * zm );
end

for i = 1: N
    for j = 1:3
        matrica (i, 1) = C  (1, i);
        matrica (i, 2) = Bz (1, i);
        matrica (i, 3) = Iz (1, i);
    end
end
```

```
figure
for i =1:N
    plot(t  , B (: ,i), 'LineWidth', 2)
    hold on
    %plot (t,  Bz (1, i)*ones(size(B (: ,i))) ,'LineWidth', 1 )

end
plot (t,  Bz (1, 10)*ones(size(B (: ,i))) ,'y','LineWidth', 2 )
title ("Change biomass over time")
    ylabel("Phytoplantkon biomass [mmol m^{-3}]")
    xlabel("Time [h]")
    grid on

figure
for i= 1:N
    plot(t , I (:, i), 'LineWidth', 2)
    hold on
    plot (t,  Iz (1, i)*ones(size(I (: ,i))) ,'LineWidth', 1 )
end
    title ("Change in irradiance over time")
    ylabel("Irradiance [W/m^2]")
    xlabel("Time [h]")
    grid on

figure
for i = 1:N
    plot(t , S (:, i), 'LineWidth', 1)
    hold on
    %plot (t,  C(1,i) ,'LineWidth', 2 )
end
plot (t,  zm*ones(size(S (: ,1)))  , 'r' , 'LineWidth',  2 )
title ("Change in S(t) over time")
    ylabel("S(t)")
    xlabel("Time [h]")
    grid on
```

```
%-----Spectral model with one phytoplankton population-------

%Cleaning memory:
clear; clc; clear vars;

%Surface irradiance:
%(I0 = 350)
I01 = 200;
I02 = 150;

%Attenuation coefficients:
%(Kw = 0.04)
Kw1 = 0.041;
Kw2 = 0.042;
k1 = 0.014;
k2 = 0.015;

% fitoplanktonska stopa rasta [m^2 /sW] :
%(alfa = 0.2)
alfa1 = 0.21;
alfa2 = 0.22;

%mp - gubici:
L = 10;

zm = 150; %mixed layer depth [m]

%Time:
dt = 0.1;  %1h [s]
T = 5;
t =  (0 : dt : T)';

%Initial conditions:
B(1,1) = (0.9).*rand(1,1);
I (1,1) = I01 * exp(- (Kw1 + k1*B(1,1) ) * zm );
I (1,2) = I02 * exp(- (Kw2 + k2*B(1,1) ) * zm );
```

```
for  n = 1 : length(t) - 1

     K1 =  Kw1 + k1*B(n,1);
     K2 =  Kw2 + k2*B(n,1);
     B (n+1,1) = B(n,1) +  ( ( alfa1*I01*B(n,1)*dt ) / ( K1 *zm ) ) * (1 - exp(-K1*zm))
+  ( ( alfa2*I02*B(n,1)*dt ) / ( K2 *zm ) ) * (1 - exp(-K2*zm))    -   L*B(n,1)* dt;
     I (n+1, 1) = I01 * exp(- (Kw1 + k1*B(n+1,1) ) * zm );
     I (n+1, 2) = I02 * exp(- (Kw2 + k2*B(n+1,1) ) * zm );

end

figure
plot(t , B (:, 1), 'r', 'LineWidth', 2)
hold on
title ("Change of biomass in time")
ylabel("Biomass [mmol m^{-3}]")
xlabel("Time [h]")
grid on

figure
plot(t  , I(:, 1), 'r' , 'LineWidth', 2)
hold on
plot(t  , I(:, 2), 'b' , 'LineWidth', 2)
title ("Change of irradiance over time")
ylabel("I(t) [W/m^2]")
xlabel("Time [h]")
grid on
legend ( 'I0 = 200 W/m^2' , 'I0 = 150 W/m^2')
```

```
%-----Spectral model with two phytoplankton population-------

%Cleaning memory:
clear; clc; clear vars;

%Surface irradiance:
%I0 = 350;  %[W/m^2]
I01 = 200;
I02 = 150;

%Attenuation coefficients:
%Kw = 0.04;
Kw1 = 0.04;
Kw2 = 0.04;
k11 = 0.05;
k12 = 0.02;
k21 = 0.02;
k22 = 0.05;

% fitoplanktonska stopa rasta [m^2 /sW]:
%alfa = 0.2;
alfa11 = 0.25;  %0.25 je granica
alfa12 = 0.10;  %0.10 je granica
alfa21 = 0.115;  %0.115 je granica
alfa22 = 0.19;  %0.203 je granica

 %mp - gubici:
%L = 10;
L1 = 10;
L2 = 10;

zm = 150; %mixed layer depth [m]

%Time:
dt = 0.1;
T = 10;
t =  (0 : dt : T)';
```

```
%Initial conditions:
B(1,1) = 0.9.*rand(1,1);
B(1,2) = B(1,1);
I (1,1) = I01 * exp(- (Kw1 + k11*B(1,1) + k12*B(1,2) ) * zm );
I (1,2) = I02 * exp(- (Kw2 + k21*B(1,1) + k22*B(1,2) ) * zm );
K1 = Kw1 + k11*B(1,1) + k12*B(1,2);
K2 = Kw2 + k21*B(1,1) + k22*B(1,2);
dBdt (1,1) = ( (alfa11*I01*B(1,1) ) / (K1 *zm) ) * ( 1 - exp (-K1 *zm ) ) +   (
(alfa12*I02*B(1,1) ) / (K2 *zm) ) * ( 1 - exp (-K2 *zm ) )  -    L1*B(1,1);
dBdt (1,2) = ( (alfa21*I01*B(1,2) ) / (K1 *zm) ) * ( 1 - exp (-K1 *zm ) ) +   (
(alfa22*I02*B(1,2) ) / (K2 *zm) ) * ( 1 - exp (-K2 *zm ) )  -    L2*B(1,2);

 for  n = 1 : length(t) - 1
    K1 = Kw1 + k11*B(n,1) + k12*B(n,2);
    K2 = Kw2 + k21*B(n,1) + k22*B(n,2);
    B (n+1,1) = B(n,1) + ( (alfa11*I01*B(n,1)*dt ) / (K1 *zm) ) * (1 - exp (-K1 *zm))
+   ( (alfa12*I02*B(n,1)*dt ) / (K2 *zm) ) * ( 1 - exp (-K2 *zm ) )  -    L1*B(n,1)*dt;
    B (n+1,2) = B(n,2) + ( (alfa21*I01*B(n,2)*dt ) / (K1 *zm) ) * (1 - exp (-K1 *zm))
+   ( (alfa22*I02*B(n,2)*dt ) / (K2 *zm) ) * ( 1 - exp (-K2 *zm ) )  -    L2*B(n,2)*dt;
    I (n+1,1) = I01 * exp(-  ( Kw1 + k11*B(n+1,1) + k12*B(n+1,2) )  * zm );
    I (n+1,2) = I02 * exp(-  ( Kw2 + k21*B(n+1,1) + k22*B(n+1,2) )  * zm );
    dBdt (n+1,1) =  ( (alfa11*I01*B(n,1) ) / (K1 *zm) ) * ( 1 - exp (-K1 *zm ) ) +
((alfa12*I02*B(n,1) ) / (K2 *zm) ) * ( 1 - exp (-K2 *zm ) )  -    L1*B(n,1);
    dBdt (n+1,2) =  ( (alfa21*I01*B(n,2) ) / (K1 *zm) ) * ( 1 - exp (-K1 *zm ) ) +
((alfa22*I02*B(n,2) ) / (K2 *zm) ) * ( 1 - exp (-K2 *zm ) )  -    L2*B(n,2);
 end

figure
plot(t  , B (:, 1), 'r' , 'LineWidth' , 2)
hold on
figure
plot(t  , B (:, 2), 'b' , 'LineWidth', 2)
title ("Change of biomass over time")
ylabel("Biomass [mmol m^{-3}]")
xlabel("Time [h]")
grid on
legend('B1' , 'B2')


[X,Y] = meshgrid(0:0.1:1, 0:0.1:1);
```

```
for i = 1:size(X,1)
    for j = 1:size(Y,2)

    K1 = Kw1 + k11*X(i,j) + k12*Y(i,j) ;
    K2 = Kw2 + k21*X(i,j) + k22*Y(i,j);
    U(i,j) = ( (alfa11*I01*X(i,j) ) / ( K1 *zm) ) * ( 1 - exp (- K1 *zm ) ) +   (
(alfa12*I02*X(i,j) ) / ( K2 *zm) ) * ( 1 - exp (- K2 *zm ) )  -    L1*X(i,j);
    V(i,j) = ( (alfa21*I01*Y(i,j) ) / (K1 *zm) ) *  ( 1 - exp (-K1 *zm ) ) +    (
(alfa22*I02*Y(i,j) ) / (K2 *zm) ) *   ( 1 - exp (-K2 *zm ) )  -    L2*Y(i,j);
    end
end

figure
plot(B(:,1), B(:,2), 'LineWidth' , 2)
 hold on
h1 = quiver (X (1:st:end, 1:st:end) , Y (1:st:end, 1:st:end), U (1:st:end, 1:st:end) ,
V (1:st:end, 1:st:end), 'r');
quiver (X,Y, U, V)
set(h1,'AutoScale','on', 'AutoScaleFactor', 10)
axis equal square
grid on
title('Dependence of biomass B_1 on biomass B_2')
xlabel("Biomass B1")
ylabel("Biomass B2")

quiver (B (:,1) , B (:,2))
quiver (B (:,1) , B (:,2), dBdt (:,1) , dBdt (:,2))
st = 10;
quiver (X1 (1:st:end, 1:st:end) , Y1 (1:st:end, 1:st:end), X2 (1:st:end, 1:st:end) ,
Y2 (1:st:end, 1:st:end))

figure
plot(t  , I (:, 1), 'r' , 'LineWidth' , 1)
hold on
plot(t  , I (:, 2), 'b' , 'LineWidth', 1)
title ("Change of irradince over time")
ylabel("Irradiance [W/m^2]")
xlabel("Time [h]")
grid on
legend('I0 = 200 W/m^2' , 'I0 = 150 W/m^2')
```

```
(*Competition model -  Mathematical Biology - An introduction - Murray 2002 *)

(*  First situation a) *)
a12 = 0.8;
a21 = 0.8;
ro=10;
ContourPlot [ { u1 *(1-u1-a12*u2) == 0 ,  ro*u2 *(1-u2-a21*u1) == 0 }, {u1,0,1.5}, {u2,0,1.5},   FrameLabel->{"u1","u2"}]

(*  Second situation b) *)
a12 = 1.8;
a21 = 1.8;
ContourPlot [ { u1 *(1-u1-a12*u2) == 0 ,  ro*u2 *(1-u2-a21*u1) == 0 }, {u1,0,1.5}, {u2,0,1.5}, FrameLabel->{"u1","u2"}]


(*  Third situation c) *)
a12 = 0.7;
a21 = 1.5;
ContourPlot [ { u1 *(1-u1-a12*u2) == 0 ,  ro*u2 *(1-u2-a21*u1) == 0 }, {u1,0,1.5}, {u2,0,1.5}, FrameLabel->{"u1","u2"}]


(*  Fourth situation d) *)
a12 = 1.5;
a21 = 0.7;
ContourPlot [ { u1 *(1-u1-a12*u2) == 0 ,  ro*u2 *(1-u2-a21*u1) == 0 }, {u1,0,1.5}, {u2,0,1.5}, FrameLabel->{"u1","u2"}]
```

(* -------Competition model for phytoplankton ----------*)

(* First case *)

```
I01 = 150;
I02 = 150;
zm = 50;
Kw1 = 0.04;
Kw2 = 0.04;
k11 = 0.01;
k12 = 0.02;
k21 = 0.02;
k22 = 0.01;
L1 = 10;
L2 = 10;
alfa11 = 0.15;
alfa12 = 0.1;
alfa21 = 0.1;
alfa22 = 0.15;

ContourPlot [ {( (alfa11*I01*B1)/( (Kw1 + k11*B1 + k12*B2)*zm) ) *(1-Exp [-(Kw1 + k11*B1 + k12*B2)*zm] ) +
   ( (alfa12*I02*B1) / ((Kw2 + k21*B1 + k22*B2)*zm ) )*(1-Exp[-(Kw2 + k21*B1 + k22*B2)*zm] ) - L1*B1 ==0 , ( (alfa21*I01*B1)/( (Kw1 + k11*B1 + k12*B2)*zm) ) *(1-Exp [-(Kw1 + k11*B1 + k12*B2)*zm] ) +
   ( (alfa22*I02*B1) / ((Kw2 + k21*B1 + k22*B2)*zm ) )*(1-Exp[-(Kw2 + k21*B1 + k22*B2)*zm] ) - L2*B1 ==0 }, {B1, 0,3} , {B2,0,3} ,   FrameLabel->{"B1(t)","B2(t)"}]
```

(* Second case *)

```
alfa11 = 0.1;
alfa12 = 0.15;
alfa21 = 0.15;
alfa22 = 0.1;

ContourPlot [ {( (alfa11*I01*B1)/( (Kw1 + k11*B1 + k12*B2)*zm) ) *(1-Exp [-(Kw1 + k11*B1 + k12*B2)*zm] ) +
   ( (alfa12*I02*B1) / ((Kw2 + k21*B1 + k22*B2)*zm ) )*(1-Exp[-(Kw2 + k21*B1 + k22*B2)*zm] ) - L1*B1 ==0 , ( (alfa21*I01*B1)/( (Kw1 + k11*B1 + k12*B2)*zm) ) *(1-Exp [-(Kw1 + k11*B1 + k12*B2)*zm] ) +
   ( (alfa22*I02*B1) / ((Kw2 + k21*B1 + k22*B2)*zm ) )*(1-Exp[-(Kw2 + k21*B1 + k22*B2)*zm] ) - L2*B1 ==0 }, {B1, 0,3} , {B2,0,3} ,  FrameLabel->{"B1(t)","B2(t)"}]
```

(*Third case*)

```
alfa11 = 0.15;
alfa12 = 0.15;
alfa21 = 0.15;
alfa22 = 0.1;

ContourPlot [ {( (alfa11*I01*B1)/( (Kw1 + k11*B1 + k12*B2)*zm) ) *(1-Exp [-(Kw1 + k11*B1 + k12*B2)*zm] ) +
    ( (alfa12*I02*B1) / ((Kw2 + k21*B1 + k22*B2)*zm ) )*(1-Exp[-(Kw2 + k21*B1 + k22*B2)*zm] ) - L1*B1 ==0 , ( (alfa21*I01*B1)/( (Kw1 + k11*B1 + k12*B2)*zm) ) *(1-Exp [-(Kw1 + k11*B1 + k12*B2)*zm] ) +
    ( (alfa22*I02*B1) / ((Kw2 + k21*B1 + k22*B2)*zm ) )*(1-Exp[-(Kw2 + k21*B1 + k22*B2)*zm] ) - L2*B1 ==0 }, {B1, 0,4} , {B2,0,4} ,  FrameLabel->{"B1(t)","B2(t)"}]
```

(*Fourth case*)

```
alfa11 = 0.1;
alfa12 = 0.15;
alfa21 = 0.15;
alfa22 = 0.15;

ContourPlot [ {( (alfa11*I01*B1)/( (Kw1 + k11*B1 + k12*B2)*zm) ) *(1-Exp [-(Kw1 + k11*B1 + k12*B2)*zm] ) +
    ( (alfa12*I02*B1) / ((Kw2 + k21*B1 + k22*B2)*zm ) )*(1-Exp[-(Kw2 + k21*B1 + k22*B2)*zm] ) - L1*B1 ==0 , ( (alfa21*I01*B1)/( (Kw1 + k11*B1 + k12*B2)*zm) ) *(1-Exp [-(Kw1 + k11*B1 + k12*B2)*zm] ) +
    ( (alfa22*I02*B1) / ((Kw2 + k21*B1 + k22*B2)*zm ) )*(1-Exp[-(Kw2 + k21*B1 + k22*B2)*zm] ) - L2*B1 ==0 }, {B1, 0,4} , {B2,0,4} ,  FrameLabel->{"B1(t)","B2(t)"}]
```