MATHEMATICAL MODELING OF CYANOBACTERIAL DYNAMICS IN A CHEMOSTAT

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ABSTRACT

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We present a mathematical model that describes how cyanobacterial communities use natural light as a source of energy and water as a source of electrons to perform photosynthesis and therefore, grow and co-survive together with other bacterial species. We apply our model to a phototrophic population of bacteria, namely, cyanobacteria. Our model involves the use of light as a source of energy and inorganic carbon as a source of nutrients. First, we study a single species model involving only cyanobacteria, then we include heterotrophs in the two species model. The model consists of ordinary differential equations describing bacteria and chemicals evolution in time. Stability analysis results show that adding heterotrophs to a population of cyanobacteria increases the level of inorganic carbon in the medium, which in turns allows cyanobacteria to perform more photosynthesis. This increase of cyanobacterial biomass agrees with experimental data obtained by collaborators at the Center for Biofilm Engineering at Montana State University.

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CHAPTER 1

INTRODUCTION

Bacterial communities exist almost everywhere in the world. They grow in both rich and poor-nutrient environments [1]. Whether bacterial communities compete or cooperate they manage to co-survive. Interactions between living micro-organisms have been mathematical modeling targets over the years. Mathematical models help understanding bacterial behaviors. In this work, we present a mathematical model describing interactions between two bacterial species living together. We apply our model to phototrophic bacteria known as cyanobacteria.

Cyanobacteria are phototrophic bacteria that contain chlorophyll allowing them to obtain their energy through photosynthesis [9][3]. Examples of these bacteria are *Synechocystis* and *Synechococcus*. Figure 1.1 depicts a growing population of cyanobacteria in lab flasks. Due to cyanobacteria's ability to fix carbon and provide nutrients it is beneficial for other organisms to live wherever cyanobacteria exist [4][8]. In some studies, cyanobacteria show an increase in growth when surrounded by heterotrophic organisms [7][15]. The aim of this work is to explain why cyanobacterial growth might increase when heterotrophs are around.

Over the years cyanobacteria have been studied in their different

Figure 1.1: This picture shows cyanobacterial colonies growing in lab flasks. The flasks are placed in a covered chamber with a continuous source of light. The picture was taken at the Center for Biofilm Engineering, Montana State University.

living forms as aggregations and in the planktonic state [11][6]. One way to study bacterial communities in their planktonic state is to use a chemostat setting. A chemostat is a bioreactor where a flow of nutrients is continuously added at a fixed rate and a mixed culture flow is removed at the same rate, keeping the culture volume constant [19][20]. For the purpose of this work, we consider a chemostat containing initial populations of cyanobacteria (autotrophs) P_1 and heterotrophs P_2. The choice of a chemostat is made in order to keep track of the nutrients in flow and the mixture out flow. A chemostat setting also allows the study of steady states. For our model, the setting can be changed and the equations can be adjusted appropriately.

Bacterial populations within the chemostat are exposed to a continuous photon inflow. A flow of inorganic carbon and oxygen is brought into the chemostat. The culture composed of bacteria and chemicals is well mixed and flows out of the chemostat at the same rate D. This process is described in Figure 1.2.

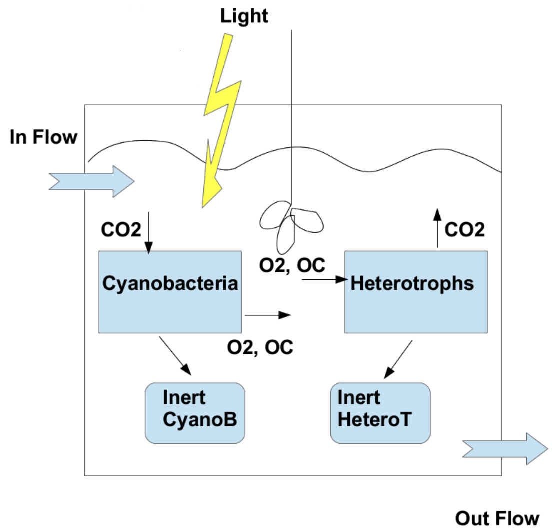


Figure 1.2: Chemostat containing bacterial populations. Oxygen and inorganic carbon are flowing in at a fixed rate. All components are well mixed and flow out at the same fixed rate.

To observe the effect of introducing heterotrophs on the growth of cyanobacteria we need to compare cyanobacterial behavior in monoculture and co-culture. For that, we present a mathematical model describing cyanobacterial growth when living alone and in the presence of heterotrophs. The model components are shown in Figure 1.3. The first model describes a chemostat containing an initial population of cyanobacteria. An amount of inorganic carbon and oxygen is continuously added to the chemostat. The mixed culture is continuously removed to keep the volume in the chemostat constant. The second model describes the same setting as the first with the addition of heterotrophs to the medium. We examine the interactions between the two populations as they co-survive. The model is initially given in terms of bacterial density then modified to represent bacterial cells in terms of carbon moles.

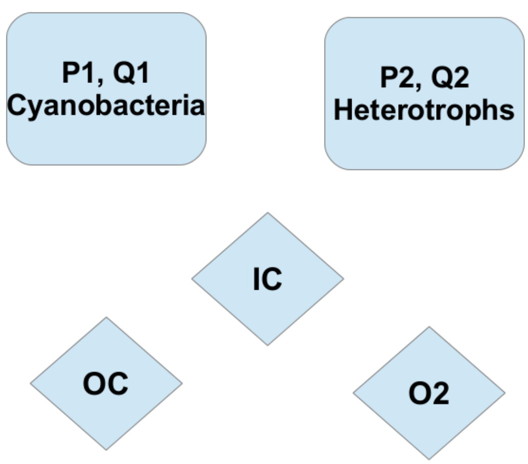


Figure 1.3: Model Components: cyanobacteria, heterotrophs, inorganic carbon, organic carbon and oxygen.

CHAPTER 2

PATHWAYS

2.1 Photosynthesis

Solar energy conversion can be performed by different photosynthetic organisms. In this work, we focus on bacterial photosynthesis and more specifically photosynthesis by cyanobacteria [4] [5].

Photosynthesis is composed of two phases. The first phase is called the light reaction. During which, cyanobacteria receive photons (ν_{light}) and use water molecules to produce oxygen and generate electrons. Each oxygen atom production requires the use of four photons as indicated in the chemical reaction given by

$$2H_2O + 4 \text{ photons} \longrightarrow 4H^+ + 4 \text{ electrons} + O_2$$

The second phase is called the dark reaction also known as the Calvin cycle. This phase is where cyanobacteria use the electrons generated during the light reaction to fix carbon. We note that some electron loss occurs between the light reaction and the dark reaction. The chemical reaction describing the dark reaction is given by

$$CO_2 + (3(1-\eta) + 4.7\eta) \text{ electrons} \longrightarrow (1-\eta)CH_2O_{1.5} + \eta CH_{1.7}O_{.5}N_{.2}$$

Cyanobacteria use the enzyme named *ribulose bisphosphate carboxylase* (RuBisCo) to either perform photosynthesis or photorespiration (a

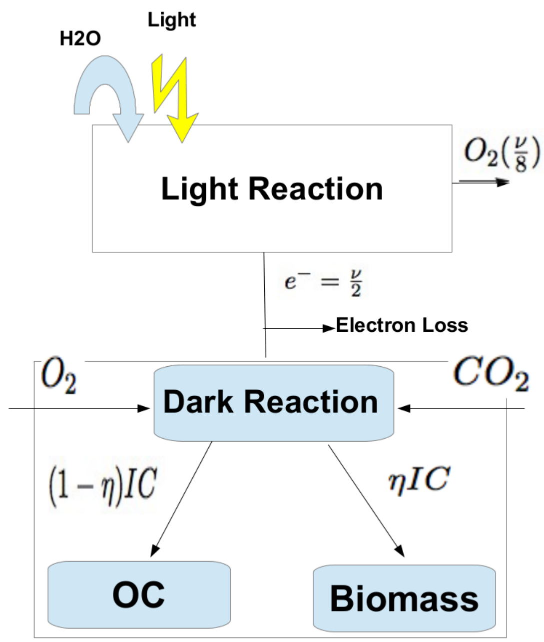


Figure 2.1: Cyanobacterial Photosynthesis Diagram

process explained in detail in Section 2.2). The chemical reaction used to describe the dark reaction is a rough estimation and only contains elements that are considered in our model. Inorganic carbon CO_2, oxygen O_2 and $(c(1-\eta)+b\eta)$ electrons are used to produce η moles of biomass and $1-\eta$ moles of organic carbon. The constants b and c are obtained from molecules/atoms degrees of reduction, which is basically how many electrons the molecule/atom is willing to receive or give away during a chemical reaction. Table 2.1 shows degrees of reduction associated to atoms used in our calculation.

Name	Atom	Degree of reduction
Carbon	C	4
Oxygen	O	-2
Hydrogen	H	1
Nitrogen	N	0

- Degree of reduction for biomass

$$CH_{1.7}O_{.5}N_{.2} \longrightarrow 4 + 1.7 - 1 - 0.2 \times (0 \textit{ or } 3) = 4.7(N_2) \textit{ or } 4.1(NH_3)$$

The quantity $CH_{1.7}O_{.5}N_{.2}$ is the molecule representing cyanobacterial biomass in the dark reaction. If cyanobacteria live in a mono-culture (by themselves) N_2 gets used but if they live in co-culture (with other organisms) NH_3 gets used instead.

- Degree of reduction for organic carbon

$$CH_2O_{1.5} \longrightarrow 2 + 4 - 3 = 3.$$

- Degree of reduction for oxygen

$$\frac{1}{2}O_2 \longrightarrow -2$$

As a result, $b = 4.1$ or 4.7 and $c = 3 + 2 = 5$

When the medium consists of both cyanobacteria and heterotrophs, the latter use oxygen and organic carbon to produce biomass and inorganic carbon according to the following reaction:

$$\begin{aligned} 2CH_2O_{1.5} + \frac{1.9}{4}O_2 &\longrightarrow CH_{1.7}O_{.5}N_{.2} + CO_2. \\ 2 + 0 &\longrightarrow 1 + 1 && \text{(Carbon Balance)} \\ 2 \times 3 + \frac{1.9}{4} \times (-4) &\longrightarrow 4.1 + 0 && \text{(Electron Balance)} \end{aligned}$$

2.2 Photorespiration

In the dark reaction, carbon fixation is controlled by the enzyme RuBisCo which catalyses the primary chemical reaction that converts inorganic carbon into biomass. However, as it happens, oxygen competes for the same binding site on RuBisCo as inorganic carbon. When a molecule of oxygen does in fact bind, then glycolate ($CH_2O_{1.5}$, degree of reduction +3) is produced instead of biomass ($CH_{1.7}O_{0.5}N_{0.2}$, degree of reduction +4.1). This process is called photorespiration, see Figure 2.2. We denote the probability of CO_2 binding to RuBisCo by

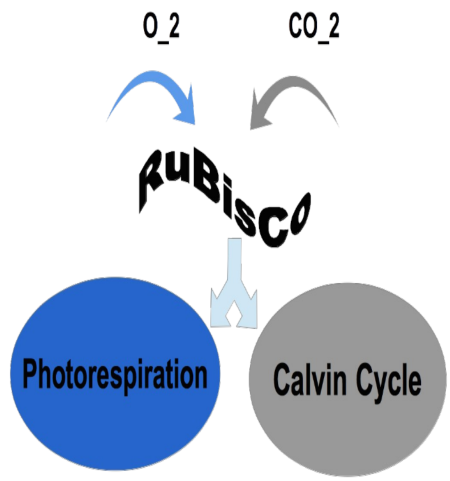


Figure 2.2: Dark reaction diagram: During the dark reaction, oxygen and inorganic carbon compete for the binding site in RuBisCo enzyme. If oxygen wins, photorespiration occurs; However, if inorganic carbon wins, then photosynthesis occurs instead.

η which is a function of CO_2 and O_2. Organisms may have a degree of control over the value of η either directly through the structure of RuBisCo itself or through indirect machinery such as carbon capture mechanisms [14] [16]. The function η is discussed in Section 3.2.

2.3 Respiration

Heterotrophs are not able to survive by themselves because they need organic components as nutrients. Cyanobacteria have the ability to fix carbon which helps heterotrophs benefit from the organic carbon and oxygen produced. Heterotrophs also provide the medium with inorganic carbon that can be used by cyanobacteria see Figure 2.3.

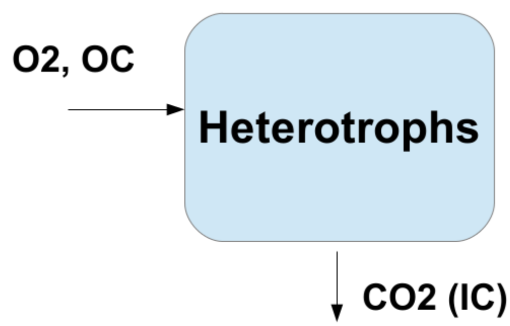


Figure 2.3: Heterotroph's respiration: heterotrophs use organic carbon and oxygen as nutrients, and produce inorganic carbon.

CHAPTER 3

KINETICS AND DYNAMICS

In this chapter we describe all the kinetics considered by our model and explain the functions used and their purposes.

3.1 Cellular carbon moles

The total mass of bacterial cells is composed of wet and dry mass. The wet mass ranges from 70% to 80% and is mostly water. The remaining volume is the dry mass, half of which is carbon while the other half is attributed to proteins and other components see Figure 3.1.

In our model, we convert bacterial densities into carbon moles. To do so we define z to be carbon moles per bacterial cell, so that zP represents carbon moles per volume. To derive the quantity z we proceed as follows,

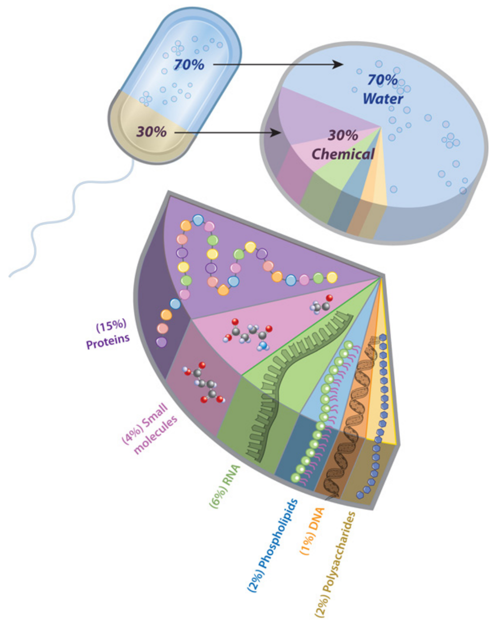


Figure 3.1: Composition of a bacterial cell. 70% the cell is water, the remaining 30% contains varying proportions of structural and functional molecules [30].

$$\begin{aligned} cell\ density &\approx 1.08 \times 10^{6} \frac{g}{m^3}, \\ \frac{volume}{cell} &\approx 5 \mu m^3 = 5 \times 10^{-18} m^3, \\ \frac{wet\ cell\ weight}{cell} &\approx 5 \times 10^{-12} \frac{g}{cell}, \\ \frac{dry\ cell\ weight}{cell} &\approx \frac{1}{5} \frac{wet\ cell\ weight}{cell} = 10^{-12} \frac{g}{cell}. \end{aligned}$$

This yields,

$$\frac{carbon\ weight}{cell} \approx \frac{1}{2} \frac{dry\ cell\ weight}{cell} = 5 \times 10^{-13} \frac{g}{cell},$$

and,

$$z \approx \frac{Cmoles}{cell} \approx \frac{carbon\ weight}{12} \approx \frac{5}{12} \times 10^{-13} \frac{g}{cell} \frac{mol}{g} = 4 \times 10^{-14} \frac{Cmoles}{cell}.$$

3.2 Probability η

In our mathematical model, we use a probability η to capture the photosynthesis and photorespiration processes. The probability is defined by

$$\eta = \frac{1}{1 + \gamma_1 \frac{O_2}{CO_2}}$$

and it describes inorganic carbon and oxygen competition for the RuBisCo binding site [14]. To derive the formula for η we first define the specificity factor γ_1 as follows

$$\gamma_1 = \frac{V_{o_2} K_{co_2}}{V_{co_2} K_{o_2}},$$

where V_{o_2} and V_{co_2} are maximum velocities of oxygenation and carboxylation. These velocities represent oxygen moles and inorganic carbon moles that the enzyme RuBisCo fixes per second. K_{o_2}, K_{co_2} are Michaelis constants for oxygen and inorganic carbon respectively [16][17]. So whether oxygen is used during the dark reaction to produce glycolate or not will be determined by the probabilities

$$\eta = \frac{\frac{V_{co_2}}{K_{co_2}} CO_2}{\frac{V_{o_2}}{K_{o_2}} O_2 + \frac{V_{co_2}}{K_{co_2}} CO_2} \quad \text{(Not using } O_2\text{)}$$

$$1 - \eta = \frac{\frac{V_{o_2}}{K_{o_2}} O_2}{\frac{V_{o_2}}{K_{o_2}} O_2 + \frac{V_{co_2}}{K_{co_2}} CO_2} \quad \text{(Using } O_2\text{)}.$$

3.3 Rate of IC transport μ_{trans}

For cyanobacteria *Synechocystis*, one bacterium contains 1.03×10^{-9} milligram of chlorophyll. The maximum transport rate of inorganic carbon is $V_{max} = 173$ micromoles per milligram of chlorophyll per hour and the half saturation rate is $K_{0.5} = 3.5\mu\ Cmole$ [12]. Using these values we obtain:

$$\begin{aligned} V_{max} &= 173 \frac{\mu mol\ of\ \mathrm{CO_2}}{mg\ Chl\ h} \\ &= \frac{173 \times 1.03 \times 10^{-9}}{3600} \frac{\mu mol\ of\ \mathrm{CO_2}}{cell\ s} \\ &= 4.95 \times 10^{-17} \frac{Cmol}{cell\ s}. \\ K_{0.5} &= 3.5\mu\ Cmole = 3.5 \times 10^{-6} Cmol. \end{aligned}$$

Throughout our work we will use the following estimated quantities

$$\begin{aligned} \mu_{trans} &= \frac{V_{max}}{z}, \\ &= \frac{4.95 \times 10^{-17}}{4 \times 10^{-14}} \frac{1}{s}, \\ &= 1.24 \times 10^{-3} \frac{1}{s}, \\ K_{trans} &= K_{0.5} = 3.5 \times 10^{-6} Cmol. \end{aligned}$$

3.4 Limiting rates e and δ

Cyanobacteria use photons ν to produce oxygen $\mathrm{O_2}$ and electrons e^-. The light intensity ν_{light} is the source of the photons ν according to the formula given by

$$\nu = \alpha\ \nu_{light}\ A$$

where, α is an efficiency factor that we set equal to 1, ν_{light} is photons per surface area per time and A is the cellular area exposed to the light. The electrons e^- are obtained using the photons ν as follows

$$e^- = Y_\nu\ \nu$$

where $Y_\nu = \frac{electron}{2\ photons}$ is a yield. The quantity $b\eta + c(1-\eta)$ is the electrons needed during the dark reaction. When light is the growth limiting factor, the function describing cyanobacterial growth rate is

$$e = \frac{e^-}{z * (b\eta + c(1-\eta))}.$$

When inorganic carbon is the growth limiting factor we set the function δ as cyanobacterial growth rate where δ is defined by

$$\delta = \mu_{trans} M(IC),$$

with μ_{trans} the maximum transport rate of inorganic carbon and M is a Monod function describing the transport rate of inorganic carbon [18],

$$M(IC) = \frac{IC}{K_{trans} + IC}.$$

3.5 Photoinhibition f

The role of the function f is to model the excess of electrons leading to bacterial damage [13] [22]. When $e - \delta < 0$, the limiting factor is inorganic carbon so there is no risk of light damage,

$$f = 1, \quad when \quad e - \delta < 0,$$

When $e - \delta > 0$, the function f is given by

$$f(e-\delta) = \frac{1}{1 + \gamma_2^2 (e-\delta)^2} \rightarrow \begin{cases} \simeq 1, \ if \ 0 \leq e - \delta \leq \dfrac{1}{\gamma_2}, \\ \rightarrow 0, \ if \ e - \delta > \dfrac{1}{\gamma_2}, \end{cases}$$

so for $e - \delta > 0$ but yet still bounded, there is no damage ($f = 1$). When $e - \delta$ is very large, f drops to zero to prevent cyanobacterial growth in the model as it is shown in the real data which motivated our choice of the photoinhibition function (see Figure 3.2).

3.6 Production rates r and r_h

Cyanobacteria grow at a rate r. The growth has two limiting factors, namely, electrons and carbon, so r is defined as,

$$r = \min(e, f\delta).$$

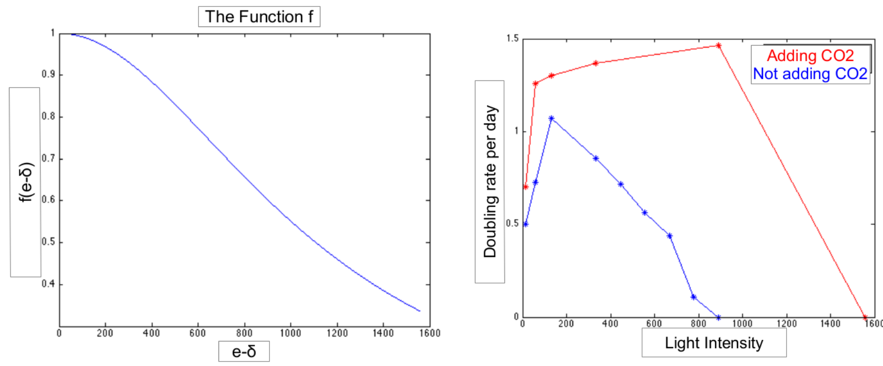


Figure 3.2: First plot is the photoinhibition function evaluated at different values of $e-\delta$. The second plot shows real data presented in [21]. The curves show cyanobacterial growth rate as a function of light intensity.

Similarly, heterotrophs grow at a rate r_h given by

$$r_h = \mu_h \min(M(OC), M(O_2)),$$

where, μ_h is heterotrophs maximum growth rate, and M is a Monod kinetic function given by,

$$M(O_2) = \frac{O_2}{K_{o_2} + O_2}, \quad M(OC) = \frac{OC}{K_{oc} + OC},$$

K_{o_2} and K_{oc} are half saturation constants for oxygen and organic carbon respectively.

Now that all model functions, variables and parameters are defined we can state our equations and explain what each term means in detail. There are two processes that describe bacterial dynamics, namely,

1. **Reproduction:** bacteria use nutrients to produce biomass and therefore grow.

2. **Inactivation:** bacteria can change from being active to being inert.

We also recall that there are three major processes that dominate the overall behavior within the chemostat setting for our model, namely,

1. **Photosynthesis:** cyanobacteria use light and inorganic carbon to produce biomass.

2. **Photorespiration:** cyanobacteria use light and oxygen to produce organic carbon.

3. **Respiration:** heterotrophs use organic carbon and oxygen to produce inorganic carbon and biomass.

In addition, all chemicals are transported in and out of the chemostat at a fixed rate, while bacteria are transported only out, at the same rate.

3.7 Bacterial Dynamics

We describe bacterial dynamics as follows,

$$
\begin{aligned}
\frac{d}{dt}\,\text{Cyano} &= (\text{Production}) - (\text{Inactivation}) - (\text{Out Flow}),\\
\frac{d}{dt}\,\text{Inert Cyano} &= (\text{Cyano Inactivation}) - (\text{Out Flow}),\\
\frac{d}{dt}\,\text{Hetero} &= (\text{Production}) - (\text{Inactivation}) - (\text{Out Flow}),\\
\frac{d}{dt}\,\text{Inert Hetero} &= (\text{Hetero Inactivation}) - (\text{Out Flow}).
\end{aligned}
$$

We represent the dynamics with the following equations,

$$
\begin{aligned}
\dot{P}_1 &= (r\eta - k_1 - D)P_1,\\
\dot{Q}_1 &= k_1 P_1 - DQ_1,\\
\dot{P}_2 &= (r_h - k_2 - D)P_2,\\
\dot{Q}_2 &= k_2 P_2 - DQ_2.
\end{aligned}
$$

3.8 Chemical Dynamics

We start with the equation describing inorganic carbon dynamics.

$$\dot{IC} = \overbrace{Y_{ic} r_h P_2}^{\text{respiration}} - \overbrace{Y_{ic} r P_1}^{\text{photosynth}} - \overbrace{D(IC - IC_0)}^{\text{chemostat transp}}. \tag{3.1}$$

When inorganic carbon successfully binds to the RuBisCo enzyme site during the dark reaction, it gets used by cyanobacteria P_1 which is represented in Equation 3.1 by the term $-Y_{ic} r P_1$. In addition, inorganic carbon is produced by heterotrophs P_2 during the respiration process $(Y_{ic} r_h P_2)$. In both the first and second terms of Equation 3.1 Y_{ic} is a yield representing carbon moles per cell. The last term in the equation represents the in and out flow of inorganic carbon through the chemostat.

Next, we explain organic carbon dynamics.

$$\dot{OC} = \overbrace{Y_{oc}(1-\eta) r P_1}^{\text{photoresp}} - \overbrace{2Y_{oc} r_h P_2}^{\text{respiration}} - \overbrace{DOC}^{\text{chemostat transp}}. \tag{3.2}$$

The first term in Equation 3.2 $(Y_{oc}(1-\eta) r P_1)$, describes production of organic carbon during photorespiration, which occurs when oxygen binds to the RuBisCo enzyme. The second term in Equation 3.2 $(2Y_{oc} r_h P_2)$ represents consumption of organic carbon during heterotrophs respiration. Similarly to inorganic carbon, the last term is the out flow through the chemostat. For organic carbon, there is no inflow through the chemostat so the only source is from production by cyanobacteria. Y_{oc} here is also carbon mole per cell.

Last, we present Equation 3.4 describing oxygen dynamics.

$$\dot{O}_2 = \overbrace{Y_{o_{21}} \nu P_1}^{\text{photosynth}} - \overbrace{Y_{o_{22}}(1-\eta) r P_1}^{\text{photoresp}} - \overbrace{Y_{o_{23}} r_h P_2}^{\text{respiration}} - \overbrace{Y_{o_{24}}(e-r)(b\eta + c(1-\eta))P_1}^{\text{electron balance}} \tag{3.3}$$

$$- \overbrace{D(O_2 - O_{2,0})}^{\text{chemostat transp}}. \tag{3.4}$$

During the light reaction, oxygen is produced by cyanobacteria. The production rate depends on photons available ν and cyanobacteria P_1. In the dark reaction, when oxygen wins the binding site in RuBisCo enzyme it gets used to produce organic carbon. This process is described by the second term ($Y_{o_{22}}(1-\eta)rP_1$) in Equation 3.4. The third term ($Y_{o_{23}}r_hP_2$) describes the use of oxygen by heterotrophs respiration. Electrons balance leads to the fourth term in Equation 3.4, namely, $Y_{o_{24}}(e-r)(b\eta+c(1-\eta))P_1$. The term $e-r$ means that we only have an electron balance when e is large enough (i.e. $e>r$) otherwise there are no electrons left to be balanced. Lastly $Y_{o_{21}}$, $Y_{o_{22}}$, $Y_{o_{23}}$ and $Y_{o_{24}}$ are yields.

Finally, our mathematical model is given by the following assembled equations,

$$
\begin{aligned}
\dot{IC} &= Y_{ic}r_hP_2 - Y_{ic}rP_1 - D(IC - IC_0),\\
\dot{OC} &= Y_{oc}(1-\eta)rP_1 - 2Y_{oc}r_hP_2 - DOC,\\
\dot{O}_2 &= Y_{o_{21}}\nu P_1 - Y_{o_{22}}(1-\eta)rP_1 - Y_{o_{23}}r_hP_2\cdots\\
&\quad - Y_{o_{24}}(e-r)(b\eta+c(1-\eta))P_1 - D(O_2 - O_{2,0}).\\
\dot{P}_1 &= (r\eta - k_1 - D)P_1,\\
\dot{Q}_1 &= k_1P_1 - DQ_1,\\
\dot{P}_2 &= (r_h - k_2 - D)P_2,\\
\dot{Q}_2 &= k_2P_2 - DQ_2,
\end{aligned}
$$

CHAPTER 4

MATHEMATICAL MODEL

Our model is a coupled system of ordinary differential equations describing interactions between cyanobacteria and heterotrophs. We consider two versions of our model, the one species case (i.e., no heterotrophs $P_2 = 0$) and the coupled model case by adding the equation for heterotrophs. For both cases, we show carbon and electrons conservation and find equilibria.

4.1 Single Species Case

The first system of odes is composed of five equations describing interactions within a chemostat. The quantities in the model are, active cyanobacteria P, inactive cyanobacteria Q, inorganic carbon IC, organic carbon OC and oxygen concentration O_2. The equations are given as follows,

$$
\begin{aligned}
\dot{IC} &= -Y_{ic} r P_1 - D(IC - IC_0),\\
\dot{OC} &= Y_{oc}(1-\eta) r P_1 - DOC,\\
\dot{O}_2 &= Y_{o_{21}} \nu P_1 - Y_{o_{22}}(1-\eta) r P_1 - Y_{o_{24}}(e-r)(b\eta + c(1-\eta))P_1\\
&\quad - D(O_2 - O_{2,0}).\\
\dot{P}_1 &= (r\eta - k_1 - D)P_1,\\
\dot{Q}_1 &= k_1 P_1 - DQ_1,
\end{aligned}
$$

we recall that $Y_{oc} = Y_{ic} = z$, $Y_{o_{21}} = \dfrac{1}{8}\dfrac{oxygen}{photons}$, $Y_{o_{22}} = \dfrac{z\; oxygen}{2\; cell}$, $Y_{o_{24}} = \dfrac{z}{4}\dfrac{oxygen}{electron}$ are all yields. Before we proceed with carbon conservation, we need to use the parameter z to convert bacterial density to carbon moles. To do so, we let $\hat{P}_1 = zP_1$ and $\hat{Q}_1 = zQ_1$ and substitute these new quantities into our model which becomes,

$$
\begin{aligned}
\dot{IC} &= -r\hat{P}_1 - D(IC - IC_0),\\
\dot{OC} &= (1-\eta) r \hat{P}_1 - DOC,\\
\dot{O}_2 &= Y_{o_{21}} \nu \frac{\hat{P}_1}{z} - Y_{o_{22}}(1-\eta) r \frac{\hat{P}_1}{z} - Y_{o_{24}}(e-r)(b\eta + c(1-\eta))\frac{\hat{P}_1}{z} - D(O_2 - O_{2,0}),\\
\dot{\hat{P}}_1 &= (r\eta - k_1 - D)\hat{P}_1,\\
\dot{\hat{Q}}_1 &= k_1 \hat{P}_1 - D\hat{Q}_1
\end{aligned}
$$

The photons ν can also be converted using the identity

$$
e = \frac{\nu\, Y_\nu}{z\,(b\eta + c(1-\eta))} = \frac{\nu\, Y_\nu}{z\,((b-c)\eta + c)}.
$$

This yields

$$
\nu = \frac{e\, z\,((b-c)\eta + c)}{Y_\nu}.
$$

Besides oxygen, all quantities are expressed in carbon moles and we can proceed with carbon conservation in the next section. Throughout the rest of this work we drop the hats.

4.1.1 Carbon Conservation

We define the carbon moles present in our system to be C. We have

$$C = P + Q + IC + OC.$$

By summing the first four equations in our system we obtain one ode describing change in carbon with time,

$$\dot{C} = -DC + DIC_0,$$

which can be solved analytically as

$$C(t) = C_0 e^{-Dt} + IC_0,$$

where C_0 is the initial amount of carbon moles in the system. The first term in the solution shows that carbon decays exponentially at a rate D. The second term is a source term, representing carbon inflow to the chemostat.

4.1.2 Electron Conservation

Here we consider our system (expressed in carbon moles) and the given number of electrons involved in each equation, namely, 4.7 for biomass (P_1 and Q_1), 0 for inorganic carbon, 3 for organic carbon and -4 for oxygen. We let E be the number of electrons involved in our system, we define

$$E = 4.7P_1 + 4.7Q_1 + 0IC + 3OC - 4O_2$$

So we use the model equations to derive an ode for E as

$$\begin{aligned}\dot{E} = &-DE - 4DO_{2,0} + [(4.7\eta + 3(1-\eta))rP_1] + [4Y_{o_{22}}(1-\eta)\frac{r}{z}P_1] \\ &+ [4Y_{o_{24}}(e-r)(4.7\eta + 3(1-\eta))\frac{P_1}{z}] - [4Y_{o_{21}}\frac{\nu}{z}P_1],\end{aligned}$$

where the first two terms between the brackets correspond, respectively, to the number of electrons used in carbon fixation and the oxygen usage;

these occur during the dark reaction. The third term in the brackets is the oxygen that binds the extra electrons available in the case of excess of light. After substituting all yields and constants, the terms in between brackets cancel each other as follows

$$
\begin{aligned}
&[(4.7\eta+3(1-\eta))rP_1]+[4Y_{o_{22}}(1-\eta)\frac{r}{z}P_1]-[4Y_{o_{21}}\frac{\nu}{z}P_1]-[4Y_{o_{24}}(r-e)(4.7\eta+3(1-\eta))\frac{P_1}{z}]\\
&=[(4.7\eta+3(1-\eta))rP_1]+[2(1-\eta)rP_1]-[\frac{\nu}{2z}P_1]-[(r-e)(4.7\eta+5(1-\eta))P_1]\\
&=[(4.7\eta+5(1-\eta))rP_1]-[\frac{e^-}{z}P_1]-[(r-e)(4.7\eta+5(1-\eta))P_1]\\
&=[(4.7\eta+5(1-\eta))rP_1]-[e(4.7\eta+5(1-\eta))P_1]-[(r-e)(4.7\eta+5(1-\eta))P_1]\\
&=0.
\end{aligned}
$$

So the equation for E is

$$\dot{E}=-DE-4DO_{2,0}$$

and can be solved as,

$$E=E_0e^{-Dt}-4O_{2,0},$$

where E_0 is the initial amount of electrons.

4.2 Coupled Model Case

For the coupled model we add an equation for heterotrophs to our system. Similarly to what we did for the first model, we would want our variables to be expressed as carbon moles. To do so, we use the following change of variables

$$\hat{P}_1=zP_1,\quad \hat{Q}_1=zQ_1,\quad \hat{P}_2=zP_2,\quad \hat{Q}_2=zQ_2,$$

to obtain

$$\dot{IC} = Y_{ic} r_h \frac{\hat{P}_2}{z} - Y_{ic} r \frac{\hat{P}_1}{z} - D(IC - IC_0),$$

$$\dot{OC} = Y_{oc}(1-\eta) r \frac{\hat{P}_1}{z} - 2Y_{oc} r_h \frac{\hat{P}_2}{z} - DOC,$$

$$\dot{O}_2 = Y_{o_{21}} \nu \frac{\hat{P}_1}{z} - Y_{o_{22}}(1-\eta) r \frac{\hat{P}_1}{z} - Y_{o_{23}} r_h \frac{\hat{P}_2}{z} - Y_{o_{24}}(e-r)(b\eta + c(1-\eta)) \frac{\hat{P}_1}{z}$$

$$-D(O_2 - O_{2,0}).$$

$$\dot{\hat{P}}_1 = (r\eta - k_1 - D)\hat{P}_1,$$

$$\dot{\hat{Q}}_1 = k_1 \hat{P}_1 - D\hat{Q}_1,$$

$$\dot{\hat{P}}_2 = (r_h - k_2 - D)\hat{P}_2,$$

$$\dot{\hat{Q}}_2 = k_2 \hat{P}_2 - D\hat{Q}_2$$

Furthermore, we drop the hats for the rest of the analysis.

4.2.1 Carbon Conservation

The process here is similar to what we did for the single species model, with the addition of an equation for heterotrophs. We let

$$C = P_1 + P_2 + Q_1 + Q_2 + OC + IC,$$

we sum up the first six equations to obtain,

$$\dot{C} = -CD + DIC_0.$$

which can be solved analytically as

$$C(t) = C_0 e^{-Dt} + IC_0.$$

4.2.2 Electron Conservation

Similarly, for electron conservation, we let

$$E = 4.1(P_1 + Q_1 + P_2 + Q_2) + 0IC + 3OC - 4O_2$$

So we have

$$\dot{E} = -DE - 4DO_{2,0} + [(4.1\eta + 3(1-\eta))rP_1] + [4Y_{o_{22}}(1-\eta)\frac{r}{z}P_1]$$
$$+ [4Y_{o_{24}}(e-r)(4.1\eta + 3(1-\eta))\frac{P_1}{z}] - [4Y_{o_{21}}\frac{\nu}{z}P_1] + [(4.1 + 4Y_{o_{23}}\frac{1}{z} - 6)r_hP_2],$$

Adding an equation for P_2 leads to a fourth term that is the electrons resulting from oxygen production during the light reaction. This term is zero,

$$(4.1 + 4Y_{o_{23}}\frac{1}{z} - 6)r_hP_2 = (4.1 + 4\frac{1.9z}{4z} - 6) = 0.$$

Now, we can solve for E as follows,

$$E = E_0e^{-Dt} - 4O_{2,0}.$$

4.3 Equilibria

At steady state, we obtain equilibrium points by setting all derivatives equal to zero. We refer to equilibria with asterisks. Bacterial equations give rise to four main cases. Below we discuss which cases are relevant to our study and those which are not possible.

Case 1 $P_1^* = 0$ & $P_2^* = 0$

This is the extinction case when no more bacteria are present in the medium at steady state. So the equilibrium we obtain is

$$P_1^* = 0,\ Q_1^* = 0,\ P_2^* = 0,\ Q_2^* = 0,\ IC^* = IC_0,\ OC^* = 0,\ O_2^* = O_{2,0}$$

Case 2 $P_1^* = 0$ & $P_2^* \neq 0$

Since $P_2^* \neq 0$ then we should have $r_h = k_2 + D$ at steady state. This gives rise to the following equilibrium

$$P_1^* = Q_1^* = 0,\ P_2^* \neq 0,\ Q_2^* = \frac{k_2}{D}P_2^*,\ IC^* = \frac{r_h}{D}P_2^* + IC_0,\ OC^* = -2\frac{r_h}{D}P_2^*,$$

$$O_2^* = -\frac{Y_{o_{23}}r_h}{zD}P_2^* + O_{2,0}.$$

This case is not possible, because it leads to a negative quantity that is supposed to be positive (OC^*). Cyanobacteria are the only source for organic carbon which is a necessary nutrients for heterotrophs to grow. So when cyanobacteria vanish, heterotrophs can no longer survive.

Case 3 $P_1^* \neq 0$ & $P_2^* = 0$

Since $P_1^* \neq 0$, it is required that $r\eta = D + k_1$ for steady state to happen. This leads to the following equilibrium

$$P_1^* \neq 0,\ Q_1^* = \frac{k_1}{D}P_1^*,\ P_2^* = Q_2^* = 0,\ IC^* = -\frac{r}{D}P_1^* + IC_0,\ OC^* = \frac{r-D}{D}P_1^*,$$

$$O_2^* = \frac{Y_{o21}\nu - Y_{o22}(r-D) - Y_{o24}(e-r)(b\eta + c(1-\eta))}{zD}P_1^* + O_{2,0}.$$

This equilibrium is when cyanobacteria reach a steady state without vanishing, while heterotrophs go to zero.

Case 4 $P_1^* \neq 0$ & $P_2^* \neq 0$

Here both P_1^* and P_2^* are non zero at steady state, therefore we have $r\eta = D + k_1$ and $r_h = D + k_2$. At equilibrium we have,

$$Q_1^* = \frac{k_1}{D}P_1^*,\ Q_2^* = \frac{k_2}{D}P_2^*,\ IC^* = -\frac{r}{D}P_1^* + \frac{r_h}{D}P_2^* + IC_0,$$

$$OC^* = \frac{r-D}{D}P_1^* - 2\frac{r_h}{D}P_2^*,$$

$$O_2^* = \frac{Y_{o21}\nu - Y_{o22}(r-D) - Y_{o24}(e-r)(b\eta + c(1-\eta))}{zD}P_1^* - \frac{Y_{o23}r_h}{zD}P_2^* + O_{2,0}.$$

This case is when both species coexist and reach steady state. Among all these equilibria we are interested most in Case 3. This case is when we add a population of heterotrophs to a medium containing cyanobacteria and study the effect that the latter has. In the following chapter we perform a stability analysis on the single species model as well as the coupled model and compare the obtained results.

4.4 Single Species vs Coupled Model

In order to understand how the presence of heterotrophs benefits cyanobacterial growth we need to investigate the steady-state case when the heterotrophs vanish and see how including their population in the medium would affect cyanobacterial population. We start by studying the single species version of the model (i.e., without heterotrophs), discuss the coupled model then compare both. For simplicity, we drop the asterisks and consider the following equations:

- The limiting factor for cyanobacterial growth is light intensity i.e.,

$$r = \min(e, f\delta) = e.$$

- We convert the photons to electrons using $\nu = \frac{e\,z\,((b-c)\eta+c)}{Y_\nu}$.
- Bacteria are considered only in their active state i.e.,

$$k_1 = k_2 = 0, \quad Q_1 = Q_2 = 0.$$

We let $X = (P_1, P_2, IC, OC, O_2)$ so that our model can be written as $\dot{X} = g(X)$ where g is the right hand side of the model. To study the stability we need the Jacobian matrix of the function g denoted Dg_1 for the first model and Dg_2 for the second model. We calculate the eigenvalues and eigenvectors, find stability condition then compare both cases. The equations of the single species model are,

$$\begin{aligned}
\dot{IC} &= -eP_1 - D(IC - IC_0),\\
\dot{OC} &= (1-\eta)eP_1 - DOC,\\
\dot{O}_2 &= \frac{Y_{o_{21}}}{Y_\nu} e\,((b-c)\eta + c)\,P_1 - \frac{Y_{o_{22}}}{z}(1-\eta)eP_1 - D(O_2 - O_{2,0}),\\
\dot{P}_1 &= (e\eta - D)P_1.
\end{aligned}$$

So Dg_1 is given by

$$\begin{bmatrix}
-D-e_{ic}P_1, & 0, & -e_{o_2}P_1, & -e,\\
(-\eta_{ic}e+(1-\eta)e_{ic})P_1, & -D, & (-\eta_{o_2}e+(1-\eta)e_{o_2})P_1, & (1-\eta)e,\\
\frac{Y_{o22}}{z}(\eta_{ic}e-e_{ic}(1-\eta))P_1\cdots & 0, & \frac{Y_{o22}}{z}(\eta_{o_2}e-e_{o_2}(1-\eta))P_1-D\cdots & \frac{Y_{o21}}{Y_\nu}e\,((b-c)\eta+c)\cdots\\
\frac{Y_{o21}}{Y_\nu}(e_{ic}((b-c)\eta+c)+(b-c)\eta_{ic}e)P_1, & & \frac{Y_{o21}}{Y_\nu}(e_{o_2}((b-c)\eta+c)+(b-c)\eta_{o_2}e)P_1, & -\frac{Y_{o22}}{z}(1-\eta)e,\\
(\eta_{ic}e+\eta e_{ic})P_1, & 0, & (\eta_{o_2}e+\eta e_{o_2})P_1, & e\eta-D,
\end{bmatrix}$$

Similarly, the equations for the coupled species model are as follows,

$$
\begin{aligned}
\dot{IC} &= r_h P_2 - eP_1 - D(IC - IC_0),\\
\dot{OC} &= (1-\eta)eP_1 - 2r_h P_2 - DOC,\\
\dot{O}_2 &= \frac{Y_{o_{21}}}{Y_\nu} e\left((b-c)\eta + c\right) P_1 - \frac{Y_{o_{22}}}{z}(1-\eta)eP_1 - \frac{Y_{o_{23}}}{z} r_h P_2 - D(O_2 - O_{2,0}),\\
\dot{P}_1 &= (e\eta - D)P_1,\\
\dot{P}_2 &= (r_h - D)P_2.
\end{aligned}
$$

This yields to the Jacobian matrix Dg_2,

$$
\begin{bmatrix}
-D-e_{ic}P_1, & r_{h_{oc}}P_2, & r_{h_{o_2}}P_2-e_{o_2}P_1, & -e, & r_h,\\
(-\eta_{ic}e+(1-\eta)e_{ic})P_1, & -D-2r_{h_{oc}}P_2, & -2r_{h_{o_2}}P_2+(-\eta_{o_2}e+(1-\eta)e_{o_2})P_1, & (1-\eta)e, & -2r_h,\\
\frac{Y_{o22}}{z}(\eta_{ic}e-e_{ic}(1-\eta))P_1\cdots & -\frac{Y_{o23}}{z}r_{h_{oc}}P_2, & -\frac{Y_{o23}}{z}r_{h_{o_2}}P_2+\frac{Y_{o22}}{z}(\eta_{o_2}e-e_{o_2}(1-\eta))P_1-D, & \frac{Y_{o21}}{Y_\nu}e\left((b-c)\eta+c\right)\cdots & -r_h\frac{Y_{o23}}{z},\\
\frac{Y_{o21}}{Y_\nu}(e_{ic}((b-c)\eta+c)+(b-c)\eta_{ic}e)P_1, & & \frac{Y_{o21}}{Y_\nu}(e_{o_2}((b-c)\eta+c)+(b-c)\eta_{o_2}e)P_1, & -\frac{Y_{o22}}{z}(1-\eta)e, & \\
(\eta_{ic}e+\eta e_{ic})P_1, & 0, & (\eta_{o_2}e+\eta e_{o_2})P_1, & e\eta-D, & 0,\\
0, & r_{h_{oc}}P_2, & r_{h_{o_2}}P_2, & 0, & r_h-D.
\end{bmatrix}
$$

We are interested in studying two equilibria, namely,

$$
\begin{aligned}
X_1^* &= (P_1^* = 0, P_2^* = 0, IC^* = IC_0, OC^* = 0, O_2^* = O_{2,0}),\\
X_2^* &= (P_1^* \neq 0, P_2^* = 0, IC^*, OC^*, O_2^*),
\end{aligned}
$$

where X_2^* components are given by

$$
\begin{aligned}
P_1^* &= \frac{-\gamma_1 D^2 zcO_{2,0} + D(e^- - Dzb)IC_0}{e(e^- - Dzb) + \gamma_1 Dc(Y_{o_{21}}\nu - Y_{o_{22}}(e-D))},\\
P_2^* &= 0,\\
IC^* &= -\frac{e}{D}P_1^* + IC_0,\\
OC^* &= \frac{(1-\eta)e}{D}P_1^*,\\
O_2^* &= \frac{Y_{o_{21}}\nu - Y_{o_{22}}(1-\eta)e}{zD}P_1^* + O_{2,0}.
\end{aligned}
$$

these values were found by solving steady state equations.

4.4.1 First Equilibrium: $X_1^* = (P_1^* = 0, P_2^* = 0, IC^*, OC^*, O_2^*)$

We linearize around X_1^* to obtain

$$Dg_1|_{X_1^*} = \begin{bmatrix} -D, & 0, & 0, & -e, \\ 0, & -D, & 0, & (1-\eta)e, \\ 0, & 0, & -D, & \frac{Y_{o21}}{z}\nu - \frac{Y_{o22}}{z}(1-\eta)e, \\ 0, & 0, & 0, & e\eta - D, \end{bmatrix}$$

then calculate the eigenvalues and corresponding eigenvectors,

$$\lambda_{1,2,3} = -D, \quad \lambda_4 = e\eta - D,$$

$$v_1 = \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \quad v_2 = \begin{pmatrix} 0 \\ 1 \\ 0 \\ 0 \end{pmatrix}, \quad v_3 = \begin{pmatrix} 0 \\ 0 \\ 1 \\ 0 \end{pmatrix}, \quad v_4 = \begin{pmatrix} -\frac{1}{\eta} \\ \frac{1-\eta}{\eta} \\ \frac{Y_{o21}\nu}{e\eta z} - \frac{Y_{o22}(1-\eta)}{\eta z} \\ 1 \end{pmatrix}.$$

The last eigenvalue is $\lambda_4 = e\eta - D$, the system is unstable if $e\eta > D$. This means that the system is unstable if cyanobacterial growth rate is larger than the wash out rate. λ_4 has a corresponding eigenspace

$$E_{e\eta-D} = \text{span}\{v_4\} = \text{span}\left\{ \begin{pmatrix} -\frac{1}{\eta} \\ \frac{1-\eta}{\eta} \\ \frac{Y_{o21}\nu}{e\eta z} - \frac{Y_{o22}(1-\eta)}{\eta z} \\ 1 \end{pmatrix} \right\},$$

The second and third components in eigenvector v_1 are positive so OC, and O_2 are increased by increasing cyanobacteria. In the mean time, the first component in the eigenvector is negative which means IC decreases as cyanobacteria increases. The second eigenvalue is $-D$, with eigenspace

$$E_{-D} = \text{span}\left\{ \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ 1 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ 0 \\ 1 \\ 0 \end{pmatrix} \right\}.$$

In this eigenspace, the component corresponding to P_1 is zero, which means that P_1 is invariant under chemicals perturbations. This is expected since we are in the extinction case. As before, we linearize the second model around X_1^* to obtain

$$Dg_2|_{X_1^*} = \begin{bmatrix} -D, & 0, & 0, & -e, & r_h, \\ 0, & -D, & 0, & (1-\eta)e, & -2r_h, \\ 0, & 0, & -D, & \frac{Y_{o21}}{z}\nu - \frac{Y_{o22}}{z}(1-\eta)e, & -r_h\frac{Y_{o23}}{z}, \\ 0, & 0, & 0, & e\eta - D, & 0, \\ 0, & 0, & 0, & 0, & r_h - D. \end{bmatrix} = \begin{bmatrix} & r_h, \\ Dg_1|_{X_1^*} & -2r_h, \\ & -r_h\frac{Y_{o23}}{z}, \\ & 0, \\ 0,\ 0,\ 0,\ 0, & r_h - D. \end{bmatrix}$$

we derive the eigenvalues, which are the same as for the single species model plus the eigenvalue corresponding to P_2 (same for eigenvectors).

$$\lambda_{1,2,3} = -D, \quad \lambda_4 = e\eta - D, \quad \lambda_5 = r_h - D.$$

The system is unstable if either $r_h > D$ or $e\eta > D$ which means that the system will be unstable if either cyanobacteria or heterotrophs growth rate is larger than the out flow rate. The corresponding eigenvectors are given by

$$v_1 = \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \quad v_2 = \begin{pmatrix} 0 \\ 1 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \quad v_3 = \begin{pmatrix} 0 \\ 0 \\ 1 \\ 0 \\ 0 \end{pmatrix}, \quad v_4 = \begin{pmatrix} -\frac{1}{\eta} \\ \frac{1-\eta}{\eta} \\ \frac{Y_{o21}\nu}{e\eta z} - \frac{Y_{o22}(1-\eta)}{\eta z} \\ 1 \\ 0 \end{pmatrix}, \quad v_5 = \begin{pmatrix} 1 \\ -2 \\ -\frac{Y_{o23}}{z} \\ 0 \\ 1 \end{pmatrix}.$$

The eigenspace of the eigenvector corresponding to $\lambda_4 = e\eta - D$ is given by

$$E_{e\eta-D} = \text{span}\{v_4\} = \text{span}\left\{\begin{pmatrix} -\frac{1}{\eta} \\ \frac{1-\eta}{\eta} \\ \frac{Y_{o21}\nu}{e\eta z} - \frac{Y_{o22}(1-\eta)}{\eta z} \\ 1 \\ 0 \end{pmatrix}\right\}.$$

The first component of v_4 being negative indicates cyanobacteria use of inorganic carbon. The second and third components being positive show organic carbon and oxygen production by cyanobacteria. Likewise, the eigenspace of the eigenvector corresponding to $\lambda_5 = r_h - D$ is

$$E_{r_h - D} = \text{span}\{v_5\} = \text{span}\left\{\begin{pmatrix} 1 \\ -2 \\ -\frac{Y_{o23}}{z} \\ 0 \\ 1 \end{pmatrix}\right\}.$$

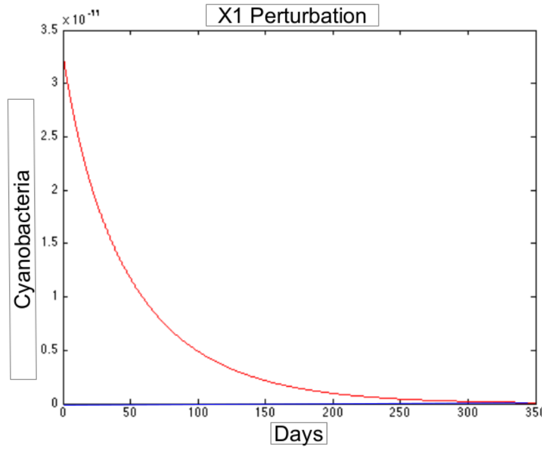
Heterotrophs produce inorganic carbon (first component of v_5 positive) and consuming inorganic carbon and oxygen (second and third components of v_5 negative). Lastly, the eigenvector corresponding the eigenvalue $\lambda_{1,2,3} = -D$ has an eigenspace given by

$$E_{-D} = \text{span}\left\{\begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ 1 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ 0 \\ 1 \\ 0 \\ 0 \end{pmatrix}\right\}.$$

In this eigenspace, the components corresponding to P_1 and P_2 are zero. Perturbations of the chemicals do not affect bacterial evolution. This is explained by the extinction of P_1 and P_2. Figure 4.1 show a small perturbation of the equilibrium X_1 in the stable case. Both cyanobacteria and heterotrophs decay until they reach $P_1 = 0$ and $P_2 = 0$.

4.4.2 Second Equilibrium: $X_2^* = (P_1^* \neq 0, P_2^* = 0, IC^*, OC^*, O_2^*)$

In this case, since $P_1^* \neq 0$ it is required at steady state that $e\eta = D$. We use the same matrices Dg_1 and Dg_2 linearized around X_2^*,



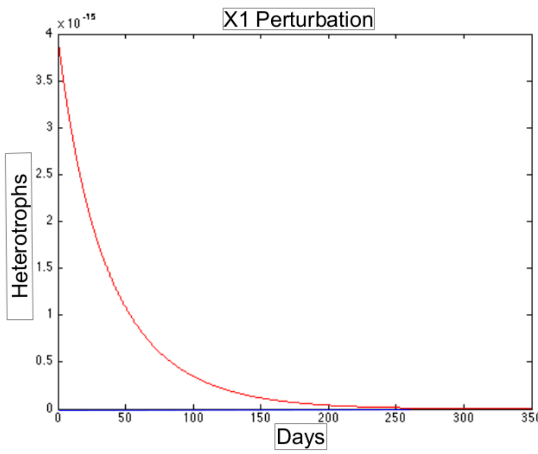


Figure 4.1: The blue curves are the numerical solutions of our coupled model starting at the equilibrium X_1^* with $P_1 = 0$ and $P_2 = 0$. The red curves are the numerical solutions of a perturbation for the equilibrium X_1^* by adding small amounts of P_1 and P_2.

respectively, as follows,

$$Dg_1|_{X_2^*} = \begin{bmatrix} -D-e_{ic}P_1, & 0, & -e_{o_2}P_1, & -e, \\ (-\eta_{ic}e+(1-\eta)e_{ic})P_1, & -D, & (-\eta_{o_2}e+(1-\eta)e_{o_2})P_1, & (1-\eta)e, \\ \frac{Y_{o22}}{z}(\eta_{ic}e-e_{ic}(1-\eta))P_1\cdots & 0, & \frac{Y_{o22}}{z}(\eta_{o_2}e-e_{o_2}(1-\eta))P_1-D\cdots & \frac{Y_{o21}}{Y_\nu}e\,((b-c)\eta+c)\cdots \\ \frac{Y_{o21}}{Y_\nu}(e_{ic}((b-c)\eta+c)+(b-c)\eta_{ic}e)P_1, & & \frac{Y_{o21}}{Y_\nu}(e_{o_2}((b-c)\eta+c)+(b-c)\eta_{o_2}e)P_1, & -\frac{Y_{o22}}{z}(1-\eta)e, \\ (\eta_{ic}e+\eta e_{ic})P_1, & 0, & (\eta_{o_2}e+\eta e_{o_2})P_1, & e\eta-D, \end{bmatrix}$$

$$Dg_2|_{X_2^*} = \begin{bmatrix} & r_h \\ Dg_1|_{X_2^*} & -2r_h \\ & -r_h\frac{Y_{o23}}{z} \\ & 0 \\ 0,\ 0,\ 0,\ 0, & r_h - D \end{bmatrix}$$

then, we obtain the following eigenvalues:

$$\textbf{For Single Species:} \quad \lambda_{1,2} = -D, \quad \lambda_{3,4}$$
$$\textbf{For Coupled Model:} \quad \lambda_{1,2} = -D, \quad \lambda_{3,4}, \quad \lambda_5 = r_h - D$$

where $\lambda_{3,4}$ are the roots of the quadratic polynomial $\lambda^2 + C_1\lambda + C_2$ with

$$C_1 = \frac{4Dez + 4e_{o_2}P_1Y_{o22}e + 4e_{ic}P_1ez - 4\eta_{o_2}P_1Y_{o22}e^2 - 4De_{o_2}P_1Y_{o22}}{4\ e\ z} \cdots$$
$$\frac{-\eta_{o_2}P_1be^2z + \eta_{o_2}P_1ce^2z - De_{o_2}P_1bz + De_{o_2}P_1cz - e_{o_2}P_1cez}{4\ e\ z}$$

$$C_2 = \frac{4\eta_{o_2}P_1Y_{o_2}e^3 + 4\eta_{ic}P_1e^3z - 4D^2e_{o_2}P_1Y_{o_2} + 4De_{ic}P_1ez - 4D\eta_{o_2}P_1Y_{o_2}e^2 - D^2e_{o_2}P_1bz}{4ez} \cdots$$
$$\frac{D^2e_{o_2}P_1cz - \eta_{o_2}P_1ce^3z - 4e_{ic}\eta_{o_2}P_1^2Y_{o_2}e^2 + 4e_{o_2}\eta_{ic}P_1^2Y_{o_2}e^2 + 4De_{o_2}P_1Y_{o_2}e - e_{ic}\eta_{o_2}P_1^2be^2z}{4ez} \cdots$$
$$\frac{e_{o_2}\eta_{ic}P_1^2be^2z + e_{ic}\eta_{o_2}P_1^2ce^2z - e_{o_2}\eta_{ic}P_1^2ce^2z - De_{o_2}P_1cez - D\eta_{o_2}P_1be^2z + D\eta_{o_2}P_1ce^2z}{4ez}$$

The single species system is unstable if $\lambda_i > 0$ for $i = 3,\ 4$. The coupled model is unstable if $\lambda_i > 0$ for $i = 3,\ 4$, or if $r_h > D$. The eigenvectors corresponding to $\lambda_i > 0$, $i = 1,\ 2$ respectively are

$$v_1 = \begin{pmatrix} 0 \\ 1 \\ 0 \\ 0 \end{pmatrix}, \quad v_2 = \begin{pmatrix} \frac{-\eta_{o_2}}{\eta_{ic}} \\ 0 \\ 1 \\ \frac{P_1(e_{ic}\eta_{o_2} - e_{o_2}\eta_{ic})}{\eta_{ic}e} \end{pmatrix}.$$

The eigenvector corresponding the eigenvalue $\lambda_{1,2} = -D$ has an eigenspace given by

$$E_{-D} = \text{span}\{v_1,\ v_2\}.$$

The eigenvalues $\lambda_{3,4}$ have corresponding eigenvectors v_3 and v_4 respectively. The eigenvector space for the coupled system is the same as the one for the single species case with an additional eigenvector v_5 corresponding to $\lambda_5 = r_h - D$. The components of the eigenvectors $v_3,\ v_4,\ v_5$ are calculated using Matlab's symbolic tools and are too long to be copied. Our focus is on the effect of heterotrophs on cyanobacteria. Therefore in the next chapter we only examine the fourth component of the eigenvector v_5.

CHAPTER 5

RESULTS AND DISCUSSION

Our results are for the case when $r = \min(e, f\delta) = e$. For both equilibria cases in the coupled model, the only eigenvector with a non-zero P_2 component is v_5 corresponding to $\lambda_5 = r_h - D$. If all eigenvalues other than λ_5 are negative we can change coordinates for our system to reduce our analysis to dynamics along v_5 (i.e a one dimensional case). We study dynamics along v_5 by examining the one dimensional ode given by,

$$\dot{v}_5 = Dg_2 v_5 = \lambda_5 v_5,$$

which can be solved as

$$v_5(t) = \exp(\lambda_5 t) v_5(0),$$

where $v_5(0)$ is the initial state. Dynamics along the span of $v_5 = \begin{pmatrix} v_{51} \\ v_{52} \\ v_{53} \\ v_{54} \\ 1 \end{pmatrix}$ show the effects of the introduction of heterotrophs on the model's other variables. We fix all parameters (see Table 5 and vary the specificity factor and light intensity and see how the fourth component v_{54} changes, where

$$
\begin{aligned}
v_{54} = \Big[&- P_1(4\eta_{o_2} Y_{o_{23}} e^2 r_h + 4\eta_{ic} e^2 r_h z - 4De_{o_2} Y_{o_{23}} r_h + 4De_{ic} r_h z - 4e_{ic}\eta_{o_2} P_1 Y_{o_{22}} e^2 \\
&- 4e_{ic}\eta_{o_2} P_1 Y_{o_{23}} e^2 + 4e_{o_2}\eta_{ic} P_1 Y_{o_2} e^2 + 4e_{o_2}\eta_{ic} P_1 Y_{o_{23}} e^2 + e_{ic}\eta_{o_2} P_1 c e^2 z \\
&- e_{o_2}\eta_{ic} P_1 c e^2 z)\Big] \Big/ \Big[4er_h^2 z + 4\eta_{o_2} P_1 Y_{o_{22}} e^3 + 4\eta_{ic} P_1 e^3 z - 4Der_h z - 4De_{o_2} P_1 Y_{o_{22}} r_h \\
&+ 4e_{o_2} P_1 Y_{o_{22}} e r_h + 4e_{ic} P_1 e r_h z - 4\eta_{o_2} P_1 Y_{o_{22}} e^2 r_h - \eta_{o_2} P_1 c e^3 z - 4e_{ic}\eta_{o_2} P_1^2 Y_{o_{22}} e^2 \\
&+ 4e_{o_2}\eta_{ic} P_1^2 Y_{o_{22}} e^2 - \eta_{o_2} P_1 b e^2 r_h z + \eta_{o_2} P_1 c e^2 r_h z - e_{ic}\eta_{o_2} P_1^2 b e^2 z + e_{o_2}\eta_{ic} P_1^2 b e^2 z \\
&+ e_{ic}\eta_{o_2} P_1^2 c e^2 z - e_{o_2}\eta_{ic} P_1^2 c e^2 z - De_{o_2} P_1 b r_h z + De_{o_2} P_1 c r_h z - e_{o_2} P_1 c e r_h z \Big]
\end{aligned}
$$

The component v_{54} is positive for different values of specificity factor and light intensity. This means that cyanobacterial biomass gets larger. Therefore our model shows that the presence of heterotrophs implies an increase in cyanobacterial biomass as observed in the lab experiment. Figure 5.2 shows a perturbation of the equilibrium X_2^*. We add a small amount of P_2 and run the code for some time. We observe that heterotrophs biomass increases and leads to an increase in cyanobacterial biomass as shown by our linearization analysis.

Our analytical analysis includes the equilibria leading to a wash out of heterotrophs. In order to discuss the equilibrium where both cyanobacteria and heterotrophs remain in the medium at steady state we proceed numerically. We solve the system of odes numerically using finite difference method. We use the same parameter values for both cases (single species and coupled model) to show cyanobacterial biomass evolution

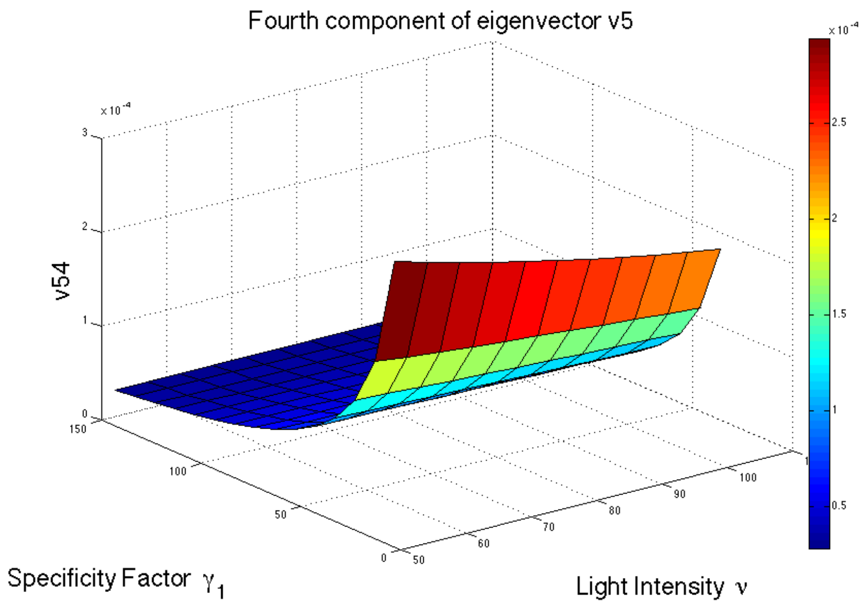


Figure 5.1: The figure shows the changes in the fourth component of the eigenvector v_5 as we vary the specificity factor γ_1 and light intensity ν_{light}

in time when the growth is limited by light at steady state.

The numerical results are presented in Figures 5.3 and 5.4. The first graph in Figure 5.3 show that cyanobacterial biomass is initially growing at the same rate for both the coupled and single species cases. As heterotroph's biomass gets larger (see the second graph in Figure 5.3) we observe an increase in cyanobacterial biomass for the coupled model case (red curve in Figure 5.3). Therefore our numerical analysis also predicts the same results as the experiment. The first graph in Figure 5.4 shows that inorganic carbon is increased due to the presence of heterotrophs which leads to an increase in cyanobacterial biomass. The second graph indicates that oxygen is increased in the coupled case. When cyanobacterial biomass increases oxygen is produced more during photosynthesis. The third graph shows that organic carbon is increased

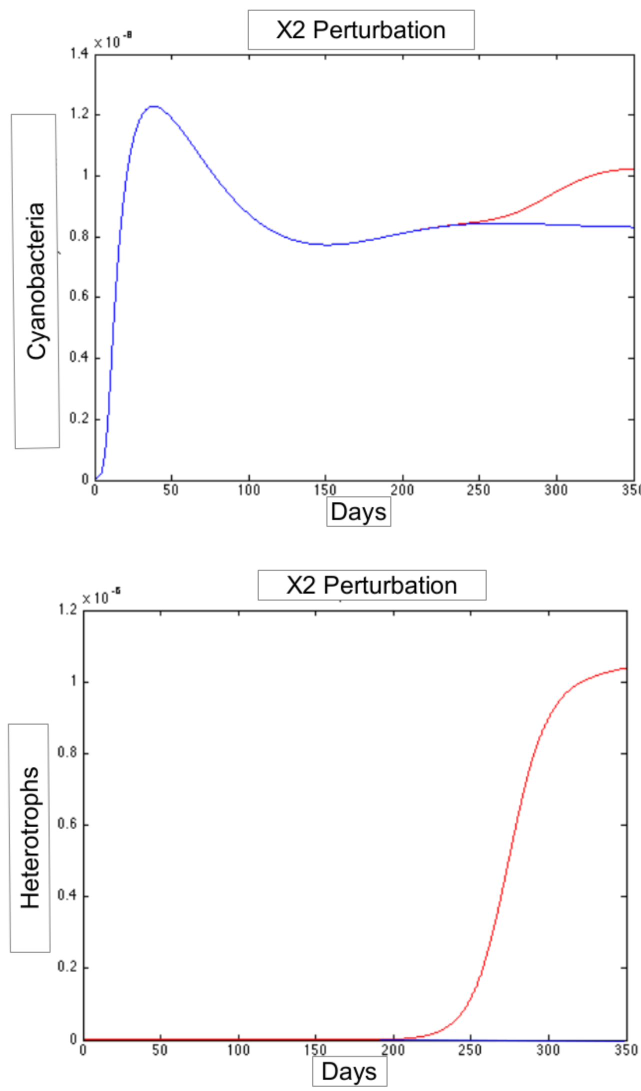


Figure 5.2: The blue curves show numerical solutions of our coupled model starting at the equilibrium X_2^* with $P_1 \neq 0$ and $P_2 = 0$. The red curves are the numerical solutions of a perturbation for the equilibrium X_2^* by adding a small amount of P_2.

at first when heterotrophs biomass is small. Then, as heterotrophs population gets larger organic carbon concentration decreases.

Our model describes the interactions between cyanobacteria and

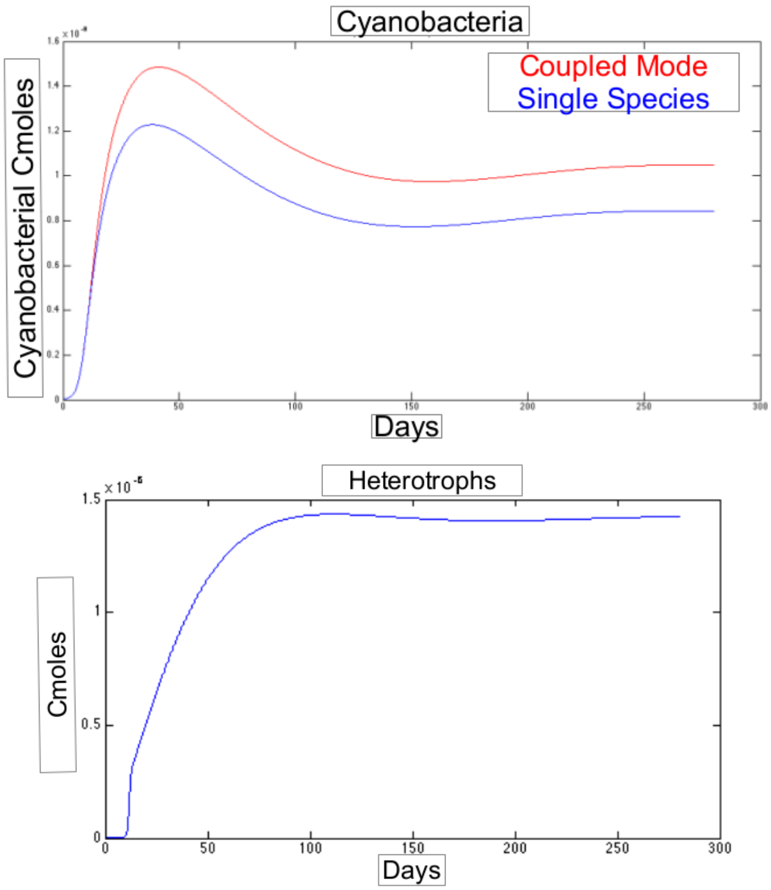


Figure 5.3: The first graph shows cyanobacterial dynamics in single species and the coupled model. The second graph shows the evolution of heterotrophs starting at a very small density.

heterotrophs. The results from the model show that after the introduction of heterotrophs to a population of cyanobacteria, there is an increase of cyanobacterial biomass. This increase of biomass agrees with data obtained by our collaborators at the Center for Biofilm Engineering at Montana State University.

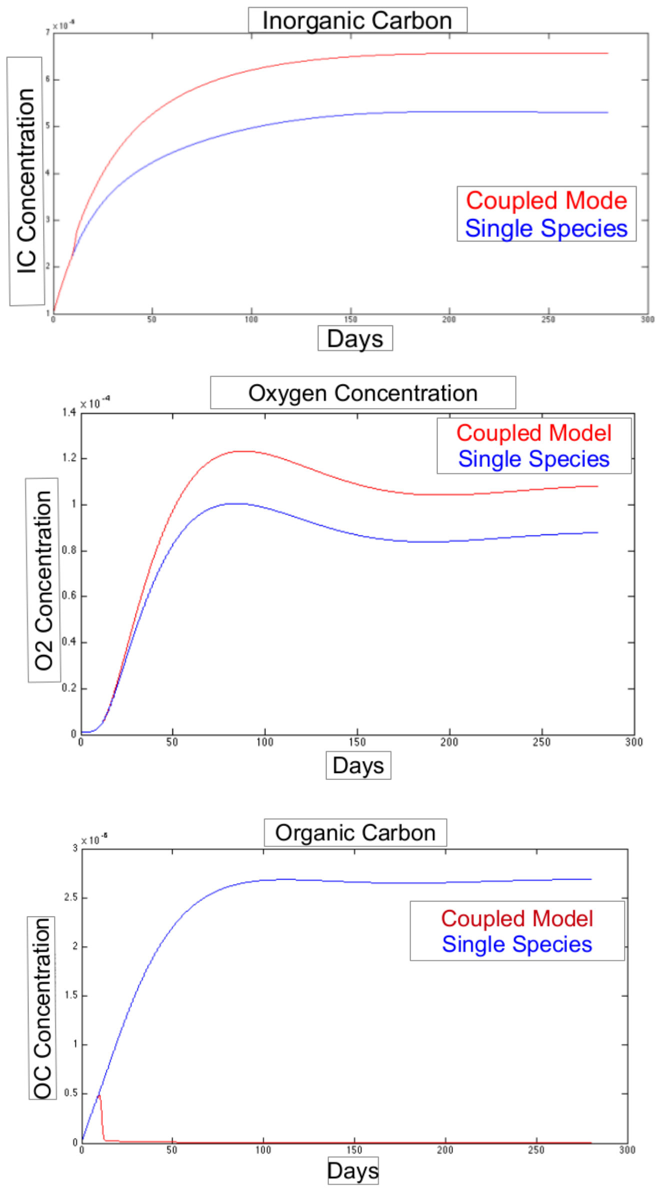


Figure 5.4: The first graph shows that inorganic carbon concentration increased when heterotrophs are introduced. The second graph shows that concentration of oxygen is slightly increased when heterotrophs are introduced. The third graph shows that organic carbon concentration is decreased from single species to the coupled case.

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PARAMETER VALUES

We present a table containing the parameters used throughout the paper with their units and values.

Symbol	**Unit**	**Value**	**Reference**
k_1,k_2	s^{-1}	.2,.1	Estimated
D	s^{-1}	.03	Estimated
z	$Cmol\ cell^{-1}$	4×10^{-14}	Calculated [10]
b	$e\ Cmol^{-1}$	4.7 or 4.1	Chem Reaction
c	$e\ Cmol^{-1}$	3	Chem Reaction
γ_1	$Cmol\ Omol^{-1}$	$9 - 15$	[14]
γ_2	s	–	–
μ_h	s^{-1}	0.0225	Measured
μ_{trans}	s^{-1}	1.24×10^{-3}	[12]
K_{trans}	$Cmol$	4.7×10^{-6}	[20]
K_{o_2}	$Omol$	8.1253×10^{-10}	[28] [27]
K_{oc}	$Cmol$	4.6022	[29]
ν_{light}	$ph(area\ s)^{-1}$	52	Measured
A	μm^2	5	–
Y_{ic}	$Cmol\ cell^{-1}$	z	$Yield$
Y_{oc}	$Cmol\ cell^{-1}$	z	$Yield$
$Y_{o_{21}}$	$Omol\ ph^{-1}$	1/8	$Yield$
$Y_{o_{22}}$	$Omol\ cell^{-1}$	$z/2$	$Yield$
$Y_{o_{23}}$	$Omol\ cell^{-1}$	$1.9\ z/4$	$Yield$
$Y_{o_{24}}$	$Omol\ electron^{-1}$	$z/4$	$Yield$
Y_ν	$Electron\ ph^{-1}$	1/2	$Yield$