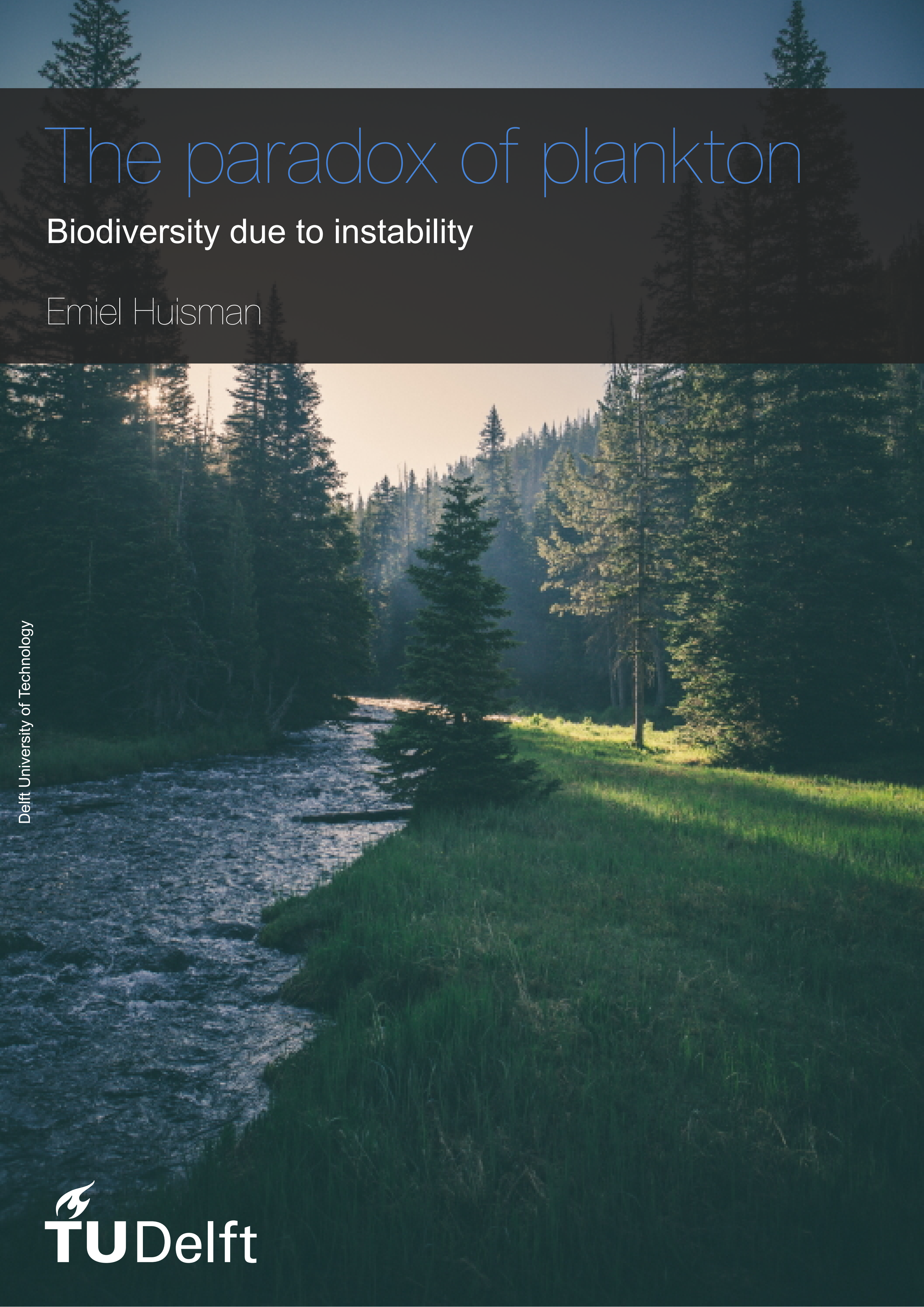

The paradox of plankton

Biodiversity due to instability

Emiel Huisman

Delft University of Technology

The paradox of plankton

Biodiversity due to instability

by

Emiel Huisman

Student Name	Student Number
E. Huisman	5135591

In partial fulfillment of the requirements for the degree of

Bachelor of Science
in Applied Physics
and
in Applied Mathematics

at the Delft University of Technology,
to be defended publicly on Friday July 8, 2022 at 13:30 AM

Supervisor Applied Mathematics:	Dr. Y. M. Dijkstra
Supervisor Applied Physics:	Dr. H. Geertsema
Thesis committee:	Dr. Ir. J. M. Thijssen
	Prof. Dr. Ir. M. van Gijzen
Project Duration:	Feb, 2022 - June, 2022

TU Delft

Abstract

The principle of competitive exclusion states that, in equilibrium, the amount of coexisting species is limited by the amount of limiting resource types in an ecosystem. However, in phytoplankton communities the paradox of plankton appears, amounts of plankton species can coexist that far exceed this upper limit.

A resource competition model is formulated and it is shown that the paradox arises for several systems, which indicates that the bloom in biodiversity is a result of the resource competition and not of any external factors. A proof is given that the principle of competitive exclusion only holds in equilibrium solutions. Therefore, as long as a system does not intersect with an equilibrium solution the biodiversity is not restricted by the amount of limiting resource types. It is concluded that intersecting with an equilibrium solution is avoided when there are only unstable equilibrium solutions present in the system. When a plankton species allows an asymptotically stable equilibrium solution, with a region of convergence equal to the domain of the system, to appear it will be called dominant. It is proven that an asymptotically stable equilibrium solution always exists in a simplified system with less than three limiting resource types. Furthermore, an algorithm is constructed that determines all the new equilibrium solutions, and their respective stabilities, when a new plankton species is introduced to a system. By applying this algorithm it can be determined whether a species is suitable for an ecosystem, when the goal is to maintain biodiversity.

The resource competition model is expanded to include light as an additional resource for all plankton species. It is observed that the coexistence of the plankton species and the total biomass is limited if there is too little light for the plankton species to consume, or if one plankton species becomes dominant due to it being significantly better at consuming light than the other species.

Additionally, the physical context of a flowing river is introduced, with dispersive and advective mass transfer and finite length. It is observed that while the spatial distribution of the plankton species along the river is strongly influenced by the spatial parameters, the biodiversity of the ecosystem is still primarily determined by the original parameters from the resource competition model, as long as the dispersive mass transfer is the dominant type of mass transfer not too large in comparison to the length of the river.

Contents

1

Introduction

In all water bodies across the earth, plankton can be found. These are microscopic or small organisms of which there are two main types. There are zooplankton, which are animals, and there are phytoplankton, which are plants (Brown, 2022). Nelson (2012) states that it is estimated that most of the oxygen in the atmosphere, 70%, is produced by marine plants, and that a significant amount of this oxygen supply is produced by phytoplankton, which sustain themselves through photosynthesis. Due to climate change, it is predicted that thermal fluctuations will increase (Easterling, 2000). Furthermore, a more biodiverse plankton community will function better under influence of these fluctuations (Bestion, 2021). Additionally, a plankton community's diversity strengthens an ecosystem's resilience and functioning (Henson et al., 2021). Therefore in the interest of sustaining the earth's oxygen supply, while also handling the impact of climate change, one should look at factors that influence the biodiversity of phytoplankton communities.

According to competition theory, the number of coexisting species, in equilibrium, cannot exceed the amount of limiting factors (Huisman & Weissing, 1999). This is called the principle of competitive exclusion. In a generic ecosystem these limiting factors are usually the individual resources that the species can consume. This forms a significant upper bound on an ecosystem's biodiversity. However, experiments have shown that phytoplankton communities often surpass this upper bound and are more diverse than previously predicted (Hutchinson, 1961). This unexpected increase in biodiversity for plankton communities, that defies the principle of competitive exclusion, is called the paradox of plankton.

Past research has proposed several solutions to the paradox. Richerson et al. (1970) proposes that when an environment has a slow mixing rate it allows several ecosystems to separately coexist. Another approach hypothesizes that an ecosystem's biodiversity is maximized when the ecosystem is externally disturbed not too little nor too frequent (Reynolds, 1993). A shared assumption in these theories is that existence of the paradox depends on external factors to the phytoplankton, such as temporal variability caused by fluctuating weather conditions or spatial heterogeneity (Huisman & Weissing, 1999).

Huisman & Weissing (1999) introduce a resource competition model , in a controlled environment, that emulates the behaviour of several plankton species competing over a limited amount of resource types. With this model it is shown that the paradox of plankton can be reproduced without invoking any external factors. Examples are given of nine phytoplankton species coexisting on three resource types. This implies that the paradox of plankton is a result of the intrinsic competitive dynamics between phytoplankton. Furthermore, due to the proposed solution to the paradox not relying on any external factors (Huisman & Weissing, 1999) it is hypothesized that this solution is broadly applicable to a vast array of other ecosystems that share characteristics with a phytoplankton community. However, to the author's knowledge, no further research has been done to validate and further analyse this proposed solution. This report serves as a mathematical complement to the model and solution to the paradox given by Huisman & Weissing (1999) with the goal of better understanding its implications. Furthermore, it motivates if, in more realistic environments, the proposed solution to the paradox given by Huisman &

Weissing (1999) is still valid.

To summarize, the goal of this paper is to answer the following research questions and sub-questions:

1. Under which conditions will the principle of competitive exclusion hold?
2. What is the combined influence of light intensity and advective and dispersive mass transfer on the existence of the paradox of plankton?
   (a) What is the influence of light intensity on the existence of the paradox of plankton?
   (b) What is the influence of advective mass transfer on the existence of the paradox of plankton?
   (c) What is the influence of dispersive mass transfer on the existence of the paradox of plankton?

Outline

In the first chapter of this report the aforementioned resource competition model is analyzed. Firstly, an algorithm is constructed that gives all the equilibrium solutions of the model. Secondly, several examples will be given that show the paradox of plankton. Thirdly, a significant new simplification of the model will be introduced and further mathematical analysis will be done to determine when the paradox of plankton fails to appear. Finally, it will be shown that the paradox of plankton can not appear in a simplified system with less than three resource types.

For this analysis the concept of a dominant species is important. When a dominant species is introduced in a pre-existing ecosystem it destroys the delicate balance between the species that were previously present. An example of a dominant species is the ring-necked parakeet, an invasive alien species which lives in many Dutch cities and towns and competes with native bird species for food and nesting space (Lawton, 2021).

In the second chapter the model will be expanded to incorporate more realistic elements. For every expansion of the model several simulations will be done to observe the effects. Firstly, light intensity will be added to the model due to all phytoplankton species using light as a shared resource. Furthermore, due to a higher density of plankton implying that every plankton absorbs less light this introduces a new oscillatory dynamic. Secondly, the system will be placed in the physical context of a river with dispersive and advective mass transfer and a constant supply of resources at the beginning of the river. This context will be incorporated in the model and the influence of the advective and dispersive mass transfer will be individually analyzed. Thirdly, light intensity and the physical context will be combined and the effect of altering the depth and background turbidity of the river will be observed.

In the discussion and conclusion the answers to the research questions will be discussed and recommendations will be given for future research.

2

Analyzing the model

2.1. Resource competition model

This section will start with a chemostat resource competition model that has been tested and verified extensively using competition experiments with phytoplankton species (Huisman & Weissing, 1999). A general discussion of this type of model can be found in Grover (1997). The model considers n plankton species and k resource types present in a bioreactor.

Chemostat is an abbreviation for a ‘chemical environment which is static‘, thus the assumption is made that the system is homogeneous and well-mixed. Further, the system is contained in a bioreactor, a vessel in which a reaction is carried out involving organisms. A schematic overview of a bioreactor is shown in figure 2.1. The bioreactor is connected to two pumps. The first pump feeds fresh material into the bioreactor, the second pump carries material out of the bioreactor.

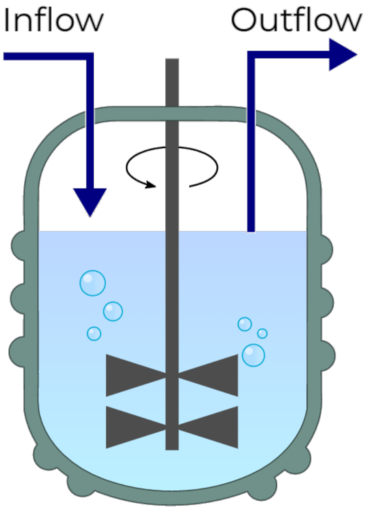

Figure 2.1: A schematic overview of a bioreactor showing the inflow and outflow of material. [15]

The bioreactor contains plankton species and resource types. The fresh material being fed into the bioreactor has a specific concentration of every resource type j, this is denoted with S_j $[\frac{kg}{m^3}]$ where $j \in \{1, 2, ..., k\}$.

The concentration of a specific plankton species i in the bioreactor is denoted with N_i $[\frac{kg}{m^3}]$, and the concentration of a specific resource type j is denoted with R_j $[\frac{kg}{m^3}]$. The goal of this section is to obtain ordinary differential equations that describe the change of R_j and N_i over time. For any quantity describing mass Q in a bioreactor the change over time can be described as (Mudde, 1998):

$$\frac{dQ}{dt} = in - out + creation - destruction$$

In this equation, in and out signify the amount of mass in the bioreactor that, over an infinitesimal amount of time, respectively enters through the inflow and leaves through the outflow. $creation$ and $destruction$ signify the amount of mass that is respectively produced or destroyed in the bioreactor, over an infinitesimal amount of time, through some other process not directly involving the inflow or outflow of the quantity of interest Q.

For the $destruction$ term, every plankton species N_i has a specific mortality rate m_i $[t^{-1}]$ and maximum specific growth rate r_i $[t^{-1}]$, where $i \in \{1, 2, ..., n\}$. For the $production$ term, every plankton species N_i has a growth rate r_i that depends on the amount of resources present in the bioreactor. The value of r_i used in the model is assumed to be for optimal circumstances when there are sufficient resources present. Furthermore, the amount of resource j in species i is described by the variable c_{ji} $[kg]$.

To examine the actual specific growth rate of a plankton species i, under the influence of limited amounts of resources, the Monod equation is used. This equation states that the actual growth rate $\boldsymbol{\mu_i}(R_j)$ of a plankton species i, when only a limited amount of resource type j is present with concentration R_j, is equal to $\frac{r_i R_j}{K_{ji}+R_j}$. Figure 2.2 shows a graphical representation of the Monod equation for several values of K_{ji}.

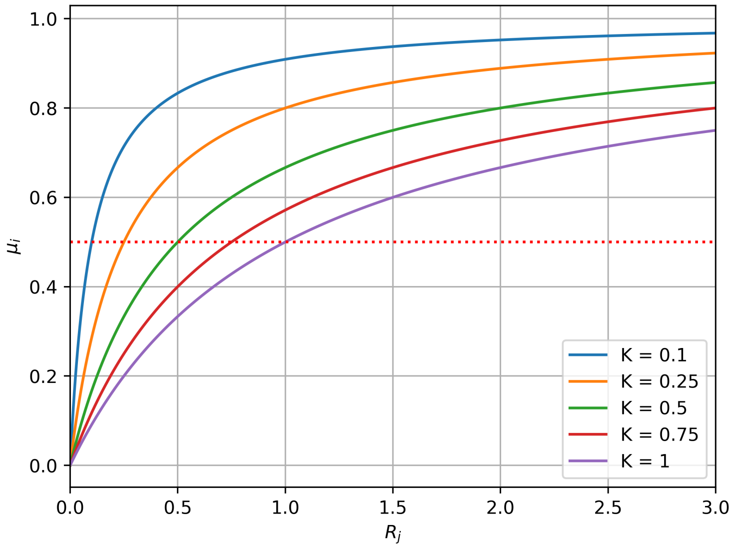

Figure 2.2: The Monod equation plotted as a function of R_j, r_i here is chosen to be equal to 1.

It is important to note that the Monod equation is concave with respect to R_j, and that $\lim_{R_j \downarrow 0} \boldsymbol{\mu_i}(R_j) = 0$ and $\lim_{R_j \to \infty} \boldsymbol{\mu_i}(R_j) = r_i$. The half-saturation constant K_{ji} is the concentration of R_j where the actual growth rate is equal to half the optimal growth rate: $\boldsymbol{\mu_i}(K_{ji}) = \frac{r_i}{2}$.

Further, to examine the actual specific growth rate of a plankton species i under the influence of multiple limiting resources, it is beneficial to look at Liebig's law of the minimum. Liebig's law states: "Growth is not dictated by the total resources available, but by the scarcest resource." (Von Liebig, 1840) In layman's terms it can be characterized by the saying: "A chain is only as strong as its weakest link." Liebig's law of the minimum is incorporated into the model in the following manner: the actual growth rate of a plankton species i when there are simultaneously k unique amounts of resources present is equal to the minimum of all the actual growth rates for every specific resource j. Reformulating this in mathematical terms gives the following expression for the actual growth rate for species i in a system of k resources:

$$\boldsymbol{\mu_i}(R_1, R_2, ..., R_k) = min(\ \boldsymbol{\mu_i}(R_1), \boldsymbol{\mu_i}(R_2), ..., \boldsymbol{\mu_i}(R_k)\ ) = min(\ \frac{r_i R_1}{K_{1i} + R_1}, ..., \frac{r_i R_k}{K_{ki} + R_k}\ ) \tag{2.1}$$

Now it is possible to construct an ordinary differential equation describing the change of N_i over time. Take $V \cdot N_i$, the total mass of a plankton species in the bioreactor, as the quantity to inspect. Where $V\ [m^3]$ is the volume in the bioreactor. Firstly, because the pumping action of the bioreactor does not affect the plankton: $in = 0$; $out = 0$. Secondly, using the previously found results and constructed variables it is possible to state: $creation = V \cdot N_i \cdot \boldsymbol{\mu_i}(R_1, R_2, ..., R_k)$; $destruction = V \cdot N_i \cdot m_i$. Combining these results gives the following ordinary differential equation describing the change of species abundance N_i over time:

$$\frac{dN_i}{dt} = N_i(\boldsymbol{\mu_i}(R_1, R_2, ..., R_k) - m_i) \tag{2.2}$$

Using equation (2.2) allows one to find the ordinary differential equation describing the change of R_j over time. First, take $V \cdot R_j$, the total mass of a resource type in the bioreactor, as the quantity to inspect. To account for the pumping speed of the inflow and outflow of the bioreactor, the turnover rate $D\ [t^{-1}]$ is introduced. D describes the fraction of volume being replaced by this pumping process over an arbitrary time frame. In this paper the arbitrary time frame will be chosen to be equal to one day. For example, $D = 0.5$ indicates that half of the system's volume is replaced every day. Start with noticing that for a period of one day, and by using the assumption that the system is well-mixed, it holds that: $in = D \cdot V \cdot S_j$; $out = D \cdot V \cdot R_j$. Furthermore, notice that during this time period some dead plankton get converted to some amount of $V \cdot R_j$ and that alive plankton take away an amount of $V \cdot R_j$, both amounts are proportional to c_{ji}. This insight allows one to state: $creation = \sum_{i=1}^{n} c_{ji} V N_i m_i$; $destruction = \sum_{i=1}^{n} c_{ji} V N_i \boldsymbol{\mu_i}(R_1, R_2, ..., R_k)$. However, Huisman & Weissing (1999) make the assumption that plankton species get converted to a new resource that is not suited for consumption, which is motivated by Grover (1997). Consequently, $creation = 0$. These results give rise to the following ordinary differential equation describing the change of resource concentration R_j over time:

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^{n} c_{ji} N_i \boldsymbol{\mu_i}(R_1, R_2, ..., R_k) \tag{2.3}$$

These two coupled ordinary differential equations (2.2-2.3) form the entire model that will be analyzed with this paper. While these equations may seem compact and unworkable, applying several analytic techniques results in rich results which will be analyzed in the next section.

2.2. Equilibrium analysis

The first step in gaining more insight into the behaviour of the chemostat model is to analyze its equilibrium solutions. By first looking at equilibrium solutions of systems with few resource types and plankton species it is possible to build up an understanding for obtaining the equilibrium solutions of a system with an arbitrary amount of resource types and plankton species.

2.2.1. 1 resource type and 1 plankton species

The goal of this section is to find values for N_1 and R_1 that satisfy $\frac{dN_1}{dt} = 0$ and $\frac{dR_1}{dt} = 0$. The first of these gives the following statement:

$$N_1 = 0 \vee \frac{r_1 R_1}{K_{11} + R_1} = m_1$$

Handling each of these 2 outcomes seperately gives:

$$\begin{cases} (N_1, R_1) = (\frac{D(S_1 - \frac{m_1 K_{11}}{r_1 - m_1})}{c_{11} m_1}, \frac{m_1 K_{11}}{r_1 - m_1}) \\ (N_1, R_1) = (0, S_1) \end{cases} \tag{2.4}$$

The first equilibrium solution is not always valid because of the physical conditions that $N_1, R_1 \geq 0$, this leads to the following parameter conditions for this solution to exist in the system:

$$\begin{cases} r_1 \geq m_1 \\ \frac{m_1}{r_1} \geq \frac{S_1}{K_{11}+S_1} \end{cases} \tag{2.5}$$

This gives the first insight, for the plankton to be able to survive in the system it is required that the ratio between the rate of plankton dying m_1 and growing r_1, under ideal circumstances, is bigger than the fraction of the supply S_1 over the sum of the half-saturation constant K_{11} and the supply S_1. One can generalize this by stating that increasing the supply of the resource R_1 makes it more likely that the plankton species N_1 survives as time progresses.

2.2.2. 1 resource types and 2 plankton species

The goal of this example is to show an example of the principle of competitive exclusion. Recall that this principle states that at most $n \leq k$ species can coexist on k limiting resources in equilibrium. The system examined has one resource type, R_1 and two plankton species N_1, N_2. The growth rate of each respective plankton species is:

$$\boldsymbol{\mu_1}(R_1) = \frac{r_1 R_1}{K_{11}+R_1} \wedge \boldsymbol{\mu_2}(R_1) = \frac{r_2 R_1}{K_{12}+R_1}$$

The equilibrium conditions $\frac{dN_1}{dt} = 0$, $\frac{dN_2}{dt} = 0$ and $\frac{dR_1}{dt} = 0$ give the following equilibrium solutions:

$$\begin{cases} (N_1, N_2, R_1) = (0, 0, S_1) \\ (N_1, N_2, R_1) = (\frac{D(S_1 - \frac{m_1 K_{11}}{r_1 - m_1})}{c_{11} m_1}, 0, \frac{m_1 K_{11}}{r_1 - m_1}) \\ (N_1, N_2, R_1) = (0, \frac{D(S_1 - \frac{m_2 K_{12}}{r_2 - m_2})}{c_{12} m_2}, \frac{m_2 K_{12}}{r_2 - m_2}) \end{cases}$$

Applying the positivity conditions that $N_1, N_2, R_1 \geq 0$ gives the same type of conditions as in the previous example. For the equilibrium solution where $N_{\boldsymbol{i}^*} = 0$, where $\boldsymbol{i}^* \in \{1, 2\}$, these are equal to:

$$\begin{cases} r_{\boldsymbol{i}^*} > m_{\boldsymbol{i}^*} \\ \frac{m_{\boldsymbol{i}^*}}{r_{\boldsymbol{i}^*}} \geq \frac{S_1}{K_{1\boldsymbol{i}^*}+S_1} \end{cases}$$

Furthermore, it is shown that it is not possible for an equilibrium solution with two plankton species to exist because there is only one resource type in the system. As a consequence, either two or one plankton species is extinct in equilibrium. This satisfies the 'principle of competitive exclusion'.

It is important to be aware that the principle is only satisfied if $\frac{m_1 K_{11}}{r_1 - m_1} \neq \frac{m_2 K_{12}}{r_2 - m_2}$. When this is not satisfied then all combinations of N_1, N_2, R_1 of the following form, that also validate the positivity conditions, also constitute a valid equilibrium solution:

$$R_1 = \frac{m_1 K_{11}}{r_1 - m_1}$$

$$D(S_1 - \frac{m_1 K_{11}}{r_1 - m_1}) = c_{11} m_1 N_1 + c_{12} m_2 N_2$$

It can be noted that this allows for an infinite amount of equilibrium solutions, because any linear combination of N_1 and N_2 that satisfied the second condition is another solution. However, this is not considered to be a concrete counter-proof to the principle of competitive exclusion. In the systems that are considered later on it is assumed that $\frac{r_1}{m_1} = \frac{r_2}{m_2}$ The condition $\frac{m_1 K_{11}}{r_1 - m_1} = \frac{m_2 K_{12}}{r_2 - m_2}$ then simplifies to the condition that $K_{11} = K_{12}$. This condition implies that the two plankton species have the same dependency on the resource R_1 and the same proportional mortality and growth rates. This indicates that the only difference between the two species are the parameters c_{11} and c_{12}, the amount of the resource R_1 that is present in N_1 and N_2. This indicates that the coexistence of these plankton species does not impact the biodiversity of the system in a meaningful way due to it resulting in two plankton species with equivalent behaviour. Because of this, with respect to biodiversity, the two plankton species can be considered to be the same and the principle of competitive exclusion is still satisfied.

2.2.3. 2 resource types and 1 plankton species

Finding the equilibrium solutions of a system with 2 resource types and 1 plankton species introduces an important new ’minimum condition’ and requires more careful analysis of the growth rate of the plankton species $\boldsymbol{\mu_1}(R_1, R_2)$. There are two possible values for this growth rate:

$$\boldsymbol{\mu_1}(R_1, R_2) = \frac{r_1 R_1}{K_{11} + R_1} \vee \boldsymbol{\mu_1}(R_1, R_2) = \frac{r_1 R_2}{K_{21} + R_2} \tag{2.6}$$

By considering each option for $\boldsymbol{\mu_1}(R_1, R_2)$ separately and finding the values that satisfy $\frac{dN_1}{dt} = 0,$ $\frac{dR_1}{dt} = 0$ and $\frac{dR_2}{dt} = 0$ the following three possible equilibrium solutions are found:

$$\begin{cases} (N_1, R_1, R_2) = (0, S_1, S_2) \\ (N_1, R_1, R_2) = (\frac{D(S_1 - \frac{m_1 K_{11}}{r_1 - m_1})}{c_{11} m_1}, \frac{m_1 K_{11}}{r_1 - m_1}, S_2 - \frac{c_{21}}{c_{11}}(S_1 - \frac{m_1 K_{11}}{r_1 - m_1})) \\ (N_1, R_1, R_2) = (\frac{D(S_2 - \frac{m_1 K_{21}}{r_1 - m_1})}{c_{21} m_1}, S_1 - \frac{c_{11}}{c_{21}}(S_2 - \frac{m_1 K_{21}}{r_1 - m_1}), \frac{m_1 K_{21}}{r_1 - m_1}) \end{cases}$$

The two equilibrium solutions, where $N_1 > 0$, only exist under specific conditions. The first three are the positivity conditions $N_1, R_1, R_2 \geq 0$. An important new condition is added which will be called the minimum condition. For each respective equilibrium solution these can be formulated as:

$$\begin{cases} \boldsymbol{\mu_1}(R_1, R_2) = \frac{r_1 R_1}{K_{11} + R_1} \Rightarrow \frac{r_1 R_1}{K_{11} + R_1} \leq \frac{r_1 R_2}{K_{21} + R_2} \\ \boldsymbol{\mu_1}(R_1, R_2) = \frac{r_1 R_2}{K_{21} + R_2} \Rightarrow \frac{r_1 R_2}{K_{21} + R_2} \leq \frac{r_1 R_1}{K_{11} + R_1} \end{cases}$$

This minimum condition guarantees that the resource values R_1, R_2 found for a specific equilibrium solution still satisfy equation (2.6). This is necessary due to the minimization function present in $\boldsymbol{\mu_1}(R_1, R_2) = min(\frac{r_1 R_1}{K_{11} + R_1}, \frac{r_1 R_2}{K_{21} + R_2})$. Inserting the found values for N_1, R_1, R_2 into these conditions, for every equilibrium solution where $N_1 > 0$, results in four inequalities which define the allowed parameters the system can have for these equilibrium solutions to be valid.

2.2.4. The trivial equilibrium solution

It is noticeable how the equilibrium solution where $N_i = 0$, for all $i \in 1, 2, ..., n$, and $R_j = S_j$, for all $j \in 1, 2, 3, ..., k$, has been present in the examples so far. This solution will be called the ‘trivial equilibrium solution‘. It can be proven that it always exists, for any arbitrary amount of plankton species and resource types, by seeing that:

$$\forall i \in \{1, 2, ..., n\}; \forall j \in \{1, 2, ..., k\};\ N_i = 0 \wedge R_j = S_j \Rightarrow \frac{dN_i}{dt} = 0 \wedge \frac{dR_j}{dt} = 0 \tag{2.7}$$

2.2.5. Arbitrary amounts of plankton species and resource types

Using the conditions and techniques that have been used so far, one can construct an algorithm that retrieves all the possible equilibrium solutions for an arbitrary system with n plankton species and k resource types. Firstly, notice that equilibrium solutions are uniquely determined by the plankton species that are present in the equilibrium and which resource type each species most depend on.

To fully encapsulate that behaviour in the equilibrium it is necessary to introduce new variables. Firstly, assume that there are $m \leq n$ plankton species which exist in the equilibrium. This leads naturally to the introduction of the variable $s_l \in \{1, 2, ...n\}$, where $l \in \{1, 2, ..., m\}$, which gives an index for all the species which exist in the equilibrium: $N_{s_l} > 0$. For all i for which there does not exist a $l \in \{1, 2, ..., m\}$ that satisfied $s_l = i$ it holds that $N_i = 0$. In total there will be $n - m$ plankton species that will be extinct in the equilibrium solution.

Secondly, for every s_l introduce a variable $q_{s_l} \in \{1, 2, ..., k\}$, which indicates the resource type $R_{q_{s_l}}$ that every non-extinct plankton species N_{s_l} growth rate most relies on:

$$\boldsymbol{\mu_{s_l}}(R_1, R_2, ..., R_k) = \frac{r_{s_l} R_{q_{s_l}}}{K_{q_{s_l} s_l} + R_{q_{s_l}}} \tag{2.8}$$

This follows from the insight in the previous section where it was observed that the growth rate of each plankton species depends on a single resource type in equilibrium. Using the newly introduced variables it is possible to find that for $\forall l \in \{1,2,...,m\}$ the equilibrium condition $\frac{dN_{s_l}}{dt} = 0$ yields:

$$R_{q_{s_l}} = \frac{m_{s_l} K_{q_{s_l} s_l}}{r_{s_l} - m_{s_l}}$$

Inserting this result into the condition $\frac{dR_{q_{s_l}}}{dt} = 0$ gives:

$$S_{q_{s_l}} - \frac{1}{D} \sum_{l*=1}^{m} c_{q_{s_l} s_{l*}} N_{s_{l*}} m_{s_{l*}} - \frac{m_{s_l} K_{q_{s_l} s_l}}{r_{s_l} - m_{s_l}} = 0 \tag{2.9}$$

To simplify the notation, introduce the variables:

$$B_l = S_{q_{s_l}} - \frac{m_{s_l} K_{q_{s_l} s_l}}{r_{s_l} - m_{s_l}} \tag{2.10}$$

$$C_{ll*} = \frac{1}{D} c_{q_{s_l} s_{l*}} m_{s_{l*}} \tag{2.11}$$

Because of those definitions it is possible to rewrite equation (2.9) as:

$$\sum_{l*=1}^{m} C_{ll*} N_{s_{l*}} = B_l \tag{2.12}$$

An essential insight here is to see that this is a linear equation. Because equation (2.12) holds for $\forall l \in \{1,2,...,m\}$ it is possible to rewrite this set of m linear equations as a single equation:

$$\begin{bmatrix} C_{11} & C_{12} & ... & C_{1m} \\ C_{21} & C_{22} & ... & C_{2m} \\ ... & ... & ... & ... \\ C_{m1} & C_{m2} & ... & C_{mm} \end{bmatrix} \cdot \begin{bmatrix} N_{s_1} \\ N_{s_2} \\ ... \\ N_{s_m} \end{bmatrix} = \begin{bmatrix} B_1 \\ B_2 \\ ... \\ B_m \end{bmatrix}$$

When the left matrix is left-invertible it is possible to solve for all N_{s_l}, where $l \in \{1,2,...,m\}$, by calculating the following vector:

$$\begin{bmatrix} N_{s_1} \\ N_{s_2} \\ ... \\ N_{s_m} \end{bmatrix} = \begin{bmatrix} C_{11} & C_{12} & ... & C_{1m} \\ C_{21} & C_{22} & ... & C_{2m} \\ ... & ... & ... & ... \\ C_{m1} & C_{m2} & ... & C_{mm} \end{bmatrix}^{-1} \cdot \begin{bmatrix} B_1 \\ B_2 \\ ... \\ B_m \end{bmatrix} \tag{2.13}$$

If the left matrix is not left-invertible it implies that there does not exist a solution where $N_{s_l} > 0$ for $\forall l \in \{1,2,...,m\}$. After having found this vector (2.13), one can calculate all R_j for which there does not exist an $l \in \{1,2,...,m\}$ that satisfies $q_{s_l} = j$, by reusing equation (2.9) in the following manner:

$$R_j = S_j - \frac{1}{D} \sum_{l*=1}^{m} c_{j s_{l*}} N_{s_{l*}} m_{s_{l*}} \tag{2.14}$$

Now all the values for $N_{s_l} > 0$, where $l \in \{1,2,...,m\}$, and R_j, where $j \in \{1,2,...,k\}$ can be computed by applying equations (2.13) and (2.14) and validated by checking if the positivity and minimum conditions are satisfied:

$$\forall i \in \{1,2,...,n\};\ N_i \leq 0$$

$$\forall j \in \{1,2,...,k\};\ R_j \leq 0$$

$$\forall l \in \{1,2,...,m\};\ \boldsymbol{\mu_{s_l}}(R_1, R_2, ..., R_k) = \frac{r_{s_l} R_{q_{s_l}}}{K_{q_{s_l} s_l} + R_{q_{s_l}}}$$

If all these conditions are satisfied a valid equilibrium solution was found for the system.

To find all the equilibrium solutions for a system with n plankton species and k resource types consider each element $\theta \in \mathbb{P}(\{1, 2, ..., n\})$, where $\mathbb{P}(S)$ denotes the powerset of the set S and a set is denoted with $\{...\}$. Furthermore, consider each element $\phi \in \mathbb{P}(\{1, 2, ..., k\})$ where $|\phi| = |\theta|$ and each associated $\delta \in Per(\phi)$, where $Per(S)$ denotes all the permutations of a set S. Repeat the steps described in this section for each δ, where $m = |\theta|$ and s_l is the l-th element of θ and q_{s_l} is the l-th element of δ, where $l \in \{1, 2, 3, m\}$, and all the possible equilibrium solutions are obtained.

For example, imagine a system with 2 plankton species and 3 resource types. Then all the possible combinations of δ and θ, for which the equilibrium solution finding algorithm is repeated, are:

m	δ	θ
0	$\emptyset$	$\emptyset$
1	$\{1\}$	$\{1\}$, $\{2\}$, $\{3\}$
1	$\{2\}$	$\{1\}$, $\{2\}$, $\{3\}$
2	$\{1, 2\}$	$\{1, 2\}$, $\{2, 1\}$, $\{1, 3\}$, $\{3, 1\}$, $\{2, 3\}$, $\{3, 2\}$

2.2.6. Proof of principle of competitive exclusion in equilibrium

Using the definitions it is possible to give a proof of the principle of competitive exclusion. To recap, the principle states that at most $n \leq k$ species can coexist on k resources in equilibrium.
Start with a system with n plankton species and k resource types, where $n > k$. Firstly, assume that for any arbitrary $j \in \{1, 2, ...k\}$ there do not exist two distinct $i, \boldsymbol{i*} \in \{1, 2, ...n\}$ for which the following is true:

$$\frac{m_i K_{ji}}{r_i - m_i} = \frac{m_{\boldsymbol{i*}} K_{j\boldsymbol{i*}}}{r_{\boldsymbol{i*}} - m_{\boldsymbol{i*}}} \tag{2.15}$$

(Otherwise there are two plankton species with equivalent behaviour which should be counted as one plankton species, with respect to biodiversity, as motivated in section (2.2.2).)

Secondly, assume that there are $k < m \leq n$ plankton species present in equilibrium. Following the same steps from the previous section, the variables $s_l \in \{1, 2, ..., n\}$, where $l \in \{1, 2, ..., m\}$, can be found for which $N_{s_l} > 0$ holds. Once again, for every s_l the variable $q_{s_l} \in \{1, 2, ..., k\}$ is introduced that satisfies equation (2.8).

An important insight is that due to $k < m$ there must be at least two plankton species which depend the most on the same resource type. This implies that there must be two distinct indices $\omega, \sigma \in \{1, 2, ..., m\}$ for which the following holds:

$$q_{s_\omega} = q_{s_\sigma} \tag{2.16}$$

Using this result in equations (2.10-2.12) gives the implication:

$$q_{s_\omega} = q_{s_\sigma} \Rightarrow C_{\omega \boldsymbol{l*}} = C_{\sigma \boldsymbol{l*}} \Rightarrow B_\omega - B_\sigma = 0$$

However, the first assumption (2.15) and equation (2.16) imply that $B_\omega - B_\sigma \neq 0$. A contradiction has been found. Due to the motivation given in section (2.2.2) the first assumption (2.15) must hold. This implies that the second assumption must be false. To conclude, there cannot be an equilibrium solution where there are $k < m \leq n$ plankton species present in the system, thus the principle of competitive exclusion is proven.

2.3. Stability of equilibrium solutions

The second step in gaining more insight into the behaviour of the chemostat model is to analyze the stability of its equilibrium solutions. The stability of an equilibrium solution has several characteristics. This section will specifically focus on whether an equilibrium point is asymptotically stable or unstable.

A asymptotically stable equilibrium acts as an attractor. It implies that once the values deviate slightly from the equilibrium, the model will bring the values back to the equilibrium. An unstable equilibrium acts as a repellor. It implies that once the values deviate slightly from the equilibrium, the values will move away further from the equilibrium.

2.3.1. Linear stability analysis

The method used to determine the stability is Jacobian stability analysis. A condition for Jacobian stability analysis is continuous derivatives. For the chemostat model that is not satisfied due to the minimum used in the definition of $\boldsymbol{\mu_i}(R_1, R_2, ..., R_k)$ in equation (2.1). However, it is assumed that for a small region around the equilibrium solution that the derivatives are continuous. This assumption is reasonable because one can imagine that there always exist a value M such that for any $\epsilon_j < M$, where $j \in \{1, 2, ..., k\}$ and $i \in \{1, 2, ..., n\}$, the following holds:

$$\boldsymbol{\mu_i}(R_1, R_2, ..., R_j, ..., R_k) = \frac{r_i R_j}{K_{ji} + R_j} \tag{2.17}$$

$$\Downarrow$$

$$\boldsymbol{\mu_i}(R_1 \pm \epsilon_1, R_2 \pm \epsilon_2, ..., R_j \pm \epsilon_3, ..., R_k \pm \epsilon_k) = \frac{r_i(R_j \pm \epsilon_j)}{K_{ji} + (R_j \pm \epsilon_j)}$$

Thus it is implied that an equilibrium solution does not lie on a coordinate where $\boldsymbol{\mu_i}(R_1, R_2, ..., R_j, ..., R_k) = \frac{r_i R_j}{K_{ji}+R_j} = \frac{r_i R_{\boldsymbol{j*}}}{K_{\boldsymbol{j*}i}+R_{\boldsymbol{j*}}}$, where $j \neq \boldsymbol{j^*} \in \{1, 2, ..., k\}$. Due to this assumption, Jacobian stability analysis is still a well-suited method to analyse the stability of the equilbrium solutions of the chemostat model.

Imagine a system with n plankton species and k resource types and an equilibrium solution with the values $(N_1, N_2, ..., N_n; R_1, R_2, ..., R_k)$. The stability of this solution can be determined by calculating the eigenvalues of the Jacobian matrix, with the inserted values of the equilibrium solution:

$$J = \begin{bmatrix}
\frac{\partial}{\partial N_1}(\frac{dN_1}{dt}) & \frac{\partial}{\partial N_2}(\frac{dN_1}{dt}) & \cdots & \frac{\partial}{\partial N_n}(\frac{dN_1}{dt}) & \frac{\partial}{\partial R_1}(\frac{dN_1}{dt}) & \frac{\partial}{\partial R_2}(\frac{dN_1}{dt}) & \cdots & \frac{\partial}{\partial R_k}(\frac{dN_1}{dt}) \\
\frac{\partial}{\partial N_1}(\frac{dN_2}{dt}) & \frac{\partial}{\partial N_2}(\frac{dN_2}{dt}) & \cdots & \frac{\partial}{\partial N_n}(\frac{dN_2}{dt}) & \frac{\partial}{\partial R_1}(\frac{dN_2}{dt}) & \frac{\partial}{\partial R_2}(\frac{dN_2}{dt}) & \cdots & \frac{\partial}{\partial R_k}(\frac{dN_2}{dt}) \\
\cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\
\frac{\partial}{\partial N_1}(\frac{dN_n}{dt}) & \frac{\partial}{\partial N_2}(\frac{dN_n}{dt}) & \cdots & \frac{\partial}{\partial N_n}(\frac{dN_n}{dt}) & \frac{\partial}{\partial R_1}(\frac{dN_n}{dt}) & \frac{\partial}{\partial R_2}(\frac{dN_n}{dt}) & \cdots & \frac{\partial}{\partial R_k}(\frac{dN_n}{dt}) \\
\frac{\partial}{\partial N_1}(\frac{dR_1}{dt}) & \frac{\partial}{\partial N_2}(\frac{dR_1}{dt}) & \cdots & \frac{\partial}{\partial N_n}(\frac{dR_1}{dt}) & \frac{\partial}{\partial R_1}(\frac{dR_1}{dt}) & \frac{\partial}{\partial R_2}(\frac{dR_1}{dt}) & \cdots & \frac{\partial}{\partial R_k}(\frac{dR_1}{dt}) \\
\frac{\partial}{\partial N_1}(\frac{dR_2}{dt}) & \frac{\partial}{\partial N_2}(\frac{dR_2}{dt}) & \cdots & \frac{\partial}{\partial N_n}(\frac{dR_2}{dt}) & \frac{\partial}{\partial R_1}(\frac{dR_2}{dt}) & \frac{\partial}{\partial R_2}(\frac{dR_2}{dt}) & \cdots & \frac{\partial}{\partial R_k}(\frac{dR_2}{dt}) \\
\cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\
\frac{\partial}{\partial N_1}(\frac{dR_k}{dt}) & \frac{\partial}{\partial N_2}(\frac{dR_k}{dt}) & \cdots & \frac{\partial}{\partial N_n}(\frac{dR_k}{dt}) & \frac{\partial}{\partial R_1}(\frac{dR_k}{dt}) & \frac{\partial}{\partial R_2}(\frac{dR_k}{dt}) & \cdots & \frac{\partial}{\partial R_k}(\frac{dR_k}{dt})
\end{bmatrix} \tag{2.18}$$

Note that the Jacobian is an $n + k$ by $n + k$ matrix and will have $\lambda_1, \lambda_2, ..., \lambda_{n+k-1}, \lambda_{n+k}$ eigenvalues. Let $Re(\lambda)$ denote the real part of an eigenvalue and let $Im(\lambda)$ denote the imaginary part.

2.3.2. Unstable and asymptotically stable equilibrium solutions

Being able to determine the stability of an equilibrium solution is important for later analysis. If for all $i \in \{1, 2, ..., n + k - 1, n + k\}$ it holds that $Re(\lambda_i) < 0$, then the equilibrium solution is asymptotically stable (Rauch, 2014). However, if there exists any $j \in \{1, 2, ..., n + k - 1, n + k\}$ for which $Re(\lambda_j) > 0$, then the equilibrium solution is unstable. Within unstable solutions there exists a difference between saddle points and purely unstable points, however that distinction will be disregarded in the following sections. Furthermore, if there exists an eigenvalue λ for which $Im(\lambda) \neq 0$ the system variables $N_1, N_2, ..., N_n, R_1, R_2, ..., R_k$ have oscillatory behaviour in a small neighbourhood around the equilibrium solution, on top of the behaviour predicted by the stability of the equilibrium.

Additionally, imagine that there is an equilibrium solution $\mathcal{E} = (N_1, N_2, ..., N_n; R_1, R_2, ...R_k)$ that is asymptotically stable. Then there exists a region $ROC \in \mathbb{R}^{n+k}$ that contains this equilibrium solution $\mathcal{E} \in ROC$. Furthermore, for any other $\mathcal{P} = (\boldsymbol{N_1^*}, \boldsymbol{N_2^*}, ..., \boldsymbol{N_n^*}; \boldsymbol{R_1^*}, \boldsymbol{R_2^*}, ...\boldsymbol{R_k^*}) \in ROC$ it holds that $\mathcal{P} \to \mathcal{E}$ as $t \to \infty$. Thus, any point initially contained in this region of convergence will eventually converge to the asymptotically stable equilibrium solution.

2.4. Behaviour predicted by the model

Now that all the techniques have been established to analyse the chemostat model, several systems can be simulated and analysed. The parameters for the systems with more than two resource types were taken from (Huisman & Weissing, 1999).

2.4.1. 2 resource types and 2 plankton species

The first example describes a system with two plankton species and two resource types. The parameters describing this system are:

D	0.25
S_1	10
S_2	10
m_1	0.25
m_2	0.25
r_1	1.00
r_2	1.00

$$K = \begin{bmatrix} 0.90 & 0.55 \\ 0.75 & 0.80 \end{bmatrix}$$

$$c = \begin{bmatrix} 0.10 & 0.25 \\ 0.05 & 0.10 \end{bmatrix}$$

$$R_{init} = \begin{bmatrix} R_1 & R_2 \end{bmatrix} = \begin{bmatrix} 10 & 10 \end{bmatrix}$$

$$N_{init} = \begin{bmatrix} N_1 & N_2 \end{bmatrix} = \begin{bmatrix} 0.11 & 0.12 \end{bmatrix}$$

The parameters K_{ji} are the values in the K matrix on the j-th row and i-th column. Similarly, the parameters c_{ji} are the values in the c matrix on the j-th row and i-th column. The initial values for the plankton species and resource types are described in the row vectors R_{init} and N_{init}, the initial value of N_1 being equal to 0.11 for example. By calculating all the equilibrium solutions with the algorithm described in (2.2.5) and applying the linear stability analysis from the previous section it is found that this system allows for only one asymptotically stable equilibrium solution to exist:

$$\begin{bmatrix} N_1 & N_2 \end{bmatrix} = \begin{bmatrix} 0.000 & 39.266 \end{bmatrix}$$

$$\begin{bmatrix} R_1 & R_2 \end{bmatrix} = \begin{bmatrix} 0.183 & 6.073 \end{bmatrix}$$

Simulating the system according to equation (2.2) and (2.3) shows the convergence to this asymptotically stable equilibrium solution, see figure 2.3.

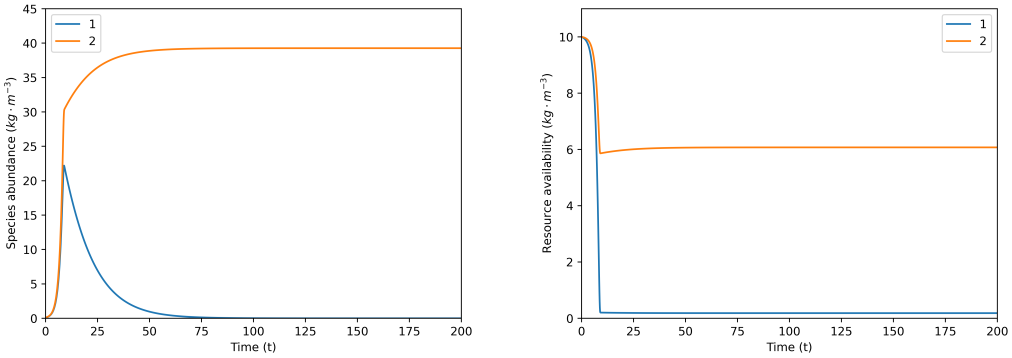

Figure 2.3: The values describing the species abundance and the resource availability over time.

Both plankton species grow simultaneously until they reach a certain size, at this point one of the two plankton species overtakes the other species and grows further, while the weaker species starts dying of at a rapid pace until it goes extinct. Thus, the convergence to a stable equilibrium is observed where one of the two plankton species goes extinct.

Furthermore, it is found that the point $(N_1, N_2; R_1, R_2) = (100, 0.12; 10, 10)$ also lies in the region of convergence of this equilibrium solution. Therefore if the initial value of N_1 is changed to 100, a significant advantage over plankton species N_2, the system will still converge to a solution where plankton species N_1 goes extinct. This behaviour can be seen in figure 2.4.

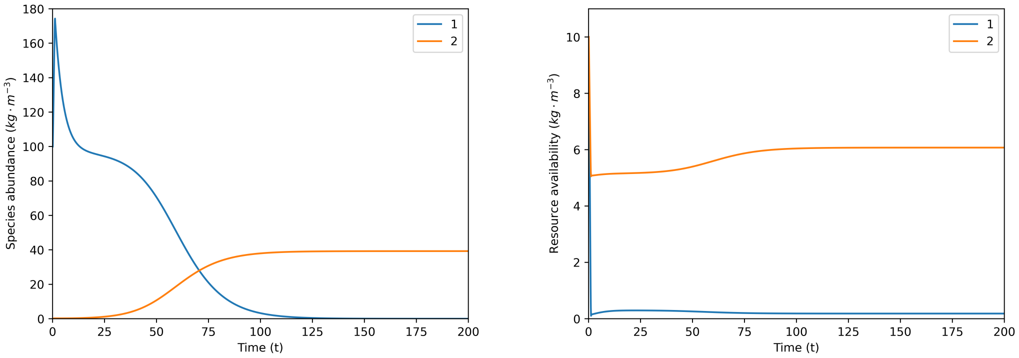

Figure 2.4: The values describing the species abundance and the resource availability over time. Note how the first plankton species N_1 starts of strong but still goes extinct as time progresses.

One plankton species starts of with a significantly bigger population size than the other plankton species. However, due to the other plankton species, with a smaller initial population size, being more dominant it eventually does overtake the other plankton species and makes it go extinct.

Now the system is altered by setting $c_{12} = 0.08$, this allows for a new set of equilibrium solutions, where the only asymptotically stable equilibrium solution is:

$$\begin{bmatrix} N_1 & N_2 \end{bmatrix} = \begin{bmatrix} 31.889 & 81.389 \end{bmatrix}$$

$$\begin{bmatrix} R_1 & R_2 \end{bmatrix} = \begin{bmatrix} 0.300 & 0.267 \end{bmatrix}$$

All the other equilibrium solutions allowed by the altered system are unstable. (In a later section (2.6.3) it will be shown that the stability of the equilibrium solutions is greatly influenced by the c_{ji} parameters.) Simulating the new system shows that the plankton species converge to this asymptotically stable equilibrium solution, see figure 2.5.

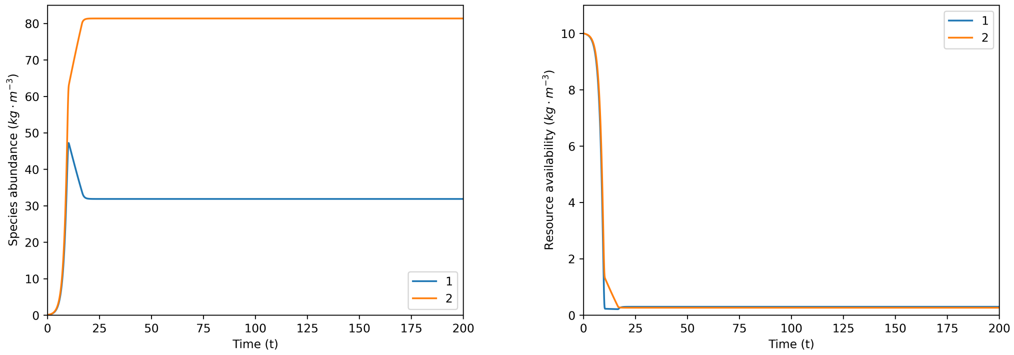

Figure 2.5: The values describing the species abundance and the resource availability over time. Note how the system approaches the previously calculated stable equilibrium solution.

Observe that more biodiversity has been added to the system by changing the c_{12} parameter. The system, with two plankton species and two resource types, converges to an equilibrium solution where both species coexist.

It is concluded that by calculating which asymptotically stable equilibrium solutions appear it is possible to predict which species can hypothetically coexist in a system. However, what happens when only unstable equilibrium solutions exist in an arbitrary system? There will be no obvious equilibrium solution the system will converge to. This question will be further investigated in the following sections.

2.4.2. 3 resource types and 3 plankton species

The second example describes a system with three plankton species and three resource types. The parameters describing this system are:

D	0.25
S_1	10
S_2	10
S_3	10
m_1	0.25
m_2	0.25
m_3	0.25
r_1	1.00
r_2	1.00
r_3	1.00

$$K = \begin{bmatrix} 1.00 & 0.75 & 0.25 \\ 0.25 & 1.00 & 0.75 \\ 0.75 & 0.25 & 1.00 \end{bmatrix}$$

$$c = \begin{bmatrix} 0.10 & 0.20 & 0.15 \\ 0.15 & 0.10 & 0.20 \\ 0.20 & 0.15 & 0.10 \end{bmatrix}$$

$$R_{init} = \begin{bmatrix} R_1 & R_2 & R_3 \end{bmatrix} = \begin{bmatrix} 10 & 10 & 10 \end{bmatrix}$$

$$N_{init} = \begin{bmatrix} N_1 & N_2 & N_3 \end{bmatrix} = \begin{bmatrix} 0.11 & 0.12 & 0.13 \end{bmatrix}$$

This system has, unlike the previous system, the property that all the equilibrium solutions found are unstable. Therefore it is not expected for the variables to converge to an equilibrium solution. In figure 2.6 it can be seen how the species have oscillatory behaviour instead.

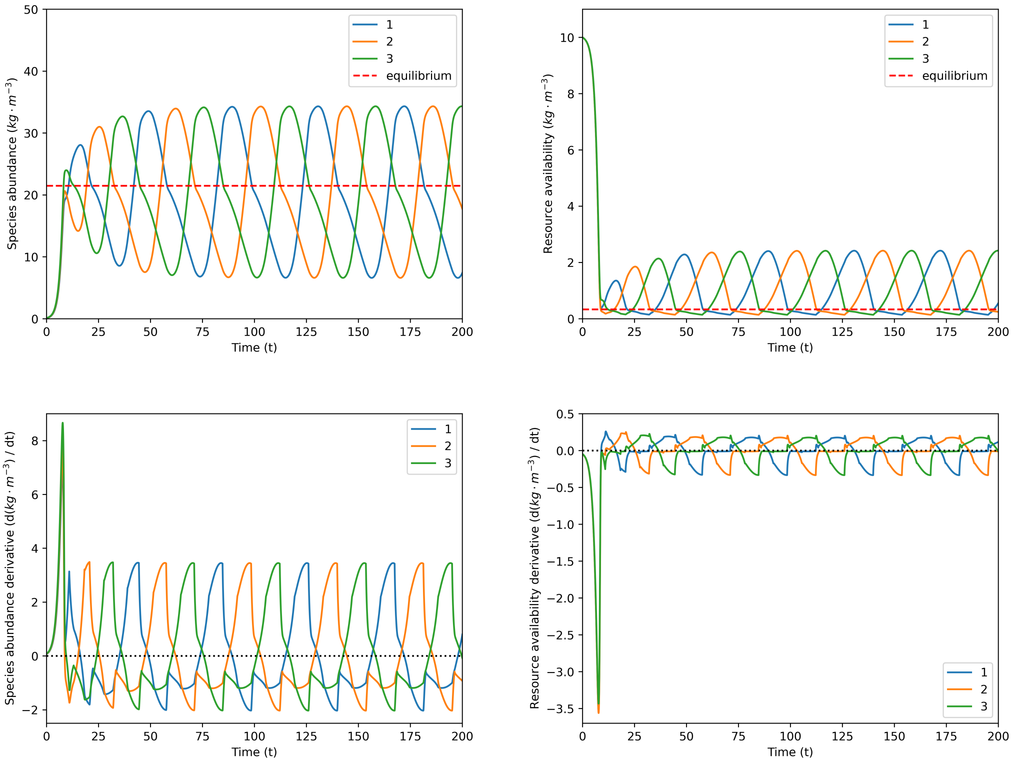

Figure 2.6: The values describing the species abundance and the resource availability over time, the respective derivatives are plotted below.

During the simulation it is observed that the plankton species, instead of converging to, oscillate around an unstable equilibrium solution. However, this equilibrium solution is not exactly in the middle of this cycle due to the non-linearity of the model. Specifically, it can be seen that the plankton species approach a limit cycle. The equilibrium point that the limit cycle oscillates around is:

$$\begin{bmatrix} N_1 & N_2 & N_3 \end{bmatrix} = \begin{bmatrix} 21.481 & 21.481 & 21.481 \end{bmatrix}$$

$$\begin{bmatrix} R_1 & R_2 & R_3 \end{bmatrix} = \begin{bmatrix} 0.333 & 0.333 & 0.333 \end{bmatrix}$$

With phase diagrams it can be visualized how the limit cycles oscillate around this equilibrium point, see figure 2.7.

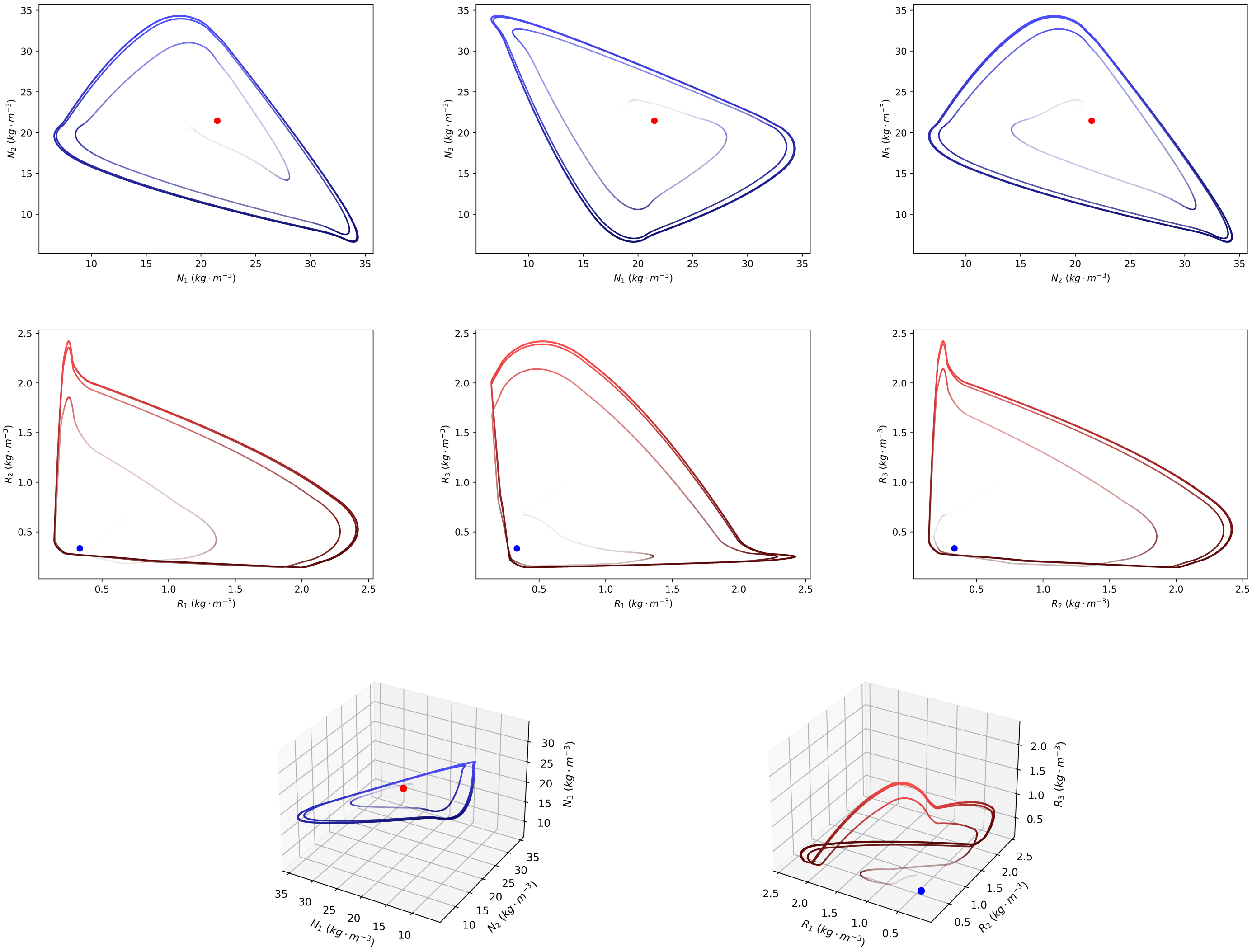

Figure 2.7: Phase diagrams representing how the plankton species and resource types approach a limit cycle over time. Observe how the equilibrium point is always contained in a orthogonal project of the limit cycles that the plankton or resources approach.

The eigenvalues, calculated with the Jacobian, belonging to this equilibrium solution are:

λ_1	$0.90625 + 5.23224i$
λ_2	$0.90625 - 5.23224i$
λ_3	-0.25000
λ_4	-0.25000
λ_5	-0.25000
λ_6	-5.43750

This implies that there are four eigenfunctions for $\lambda_3, \lambda_4, \lambda_5, \lambda_6$ which approach the equilibrium. However, there are also two unstable eigenfunctions for λ_1, λ_2 which oscillate around the equilibrium.

Further analyzing the behaviour of the limit cycle, the parameter K_{11} is systematically altered. This results in several bifurcation graphs, shown in figure 2.8, which shows the minimum and maximum value of the limit cycle, given that it exists, and its associated equilibrium solution as the red dotted line.

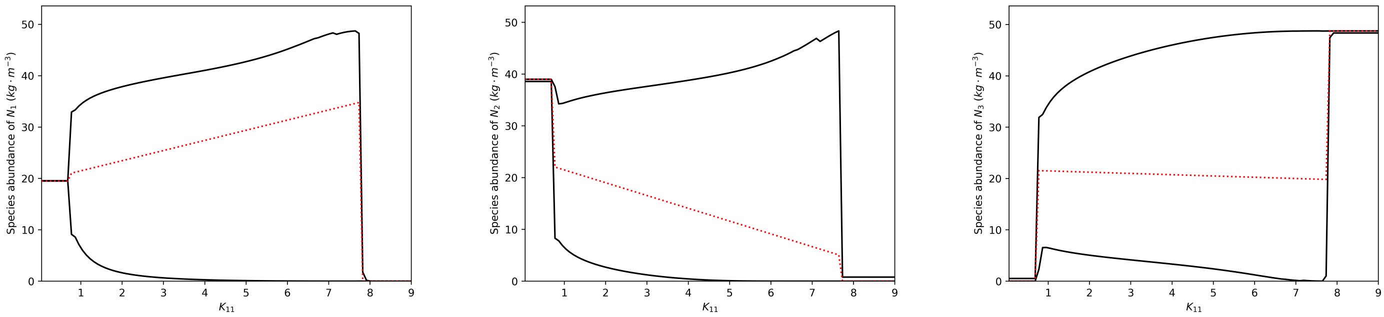

Figure 2.8: Bifurcation graphs showing the dimensions of the limit cycles, if they exist, for each plankton species for several values of K_{11}. Notice how the limit cycle only exists for a specific range of values for K_{11}.

It can be observed how the stability of the equilibrium solutions of the system changes when K_{11} decreases below 0.75. The reason for this is that this introduces a new asymptotically stable equilibrium solution. For example, when $K_{11} = 0.74$ this solution is:

$$\begin{bmatrix} N_1 & N_2 & N_3 \end{bmatrix} = \begin{bmatrix} 19.500 & 39.000 & 0.000 \end{bmatrix}$$

$$\begin{bmatrix} R_1 & R_2 & R_3 \end{bmatrix} = \begin{bmatrix} 0.250 & 3.175 & 0.250 \end{bmatrix}$$

Furthermore, different types of oscillations may appear (Huisman & Weissing, 2002b). Revert K_{11} back to 1.00 and introduce the following parameter variations:

$$K = \begin{bmatrix} 1.00 & \alpha & 0.25 \\ 0.25 & 1.00 & \alpha \\ \alpha & 0.25 & 1.00 \end{bmatrix}$$

When $0.25 < \alpha < 1.00$ the system still only has unstable equilibrium solutions. Outside of this range an undesired asymptotically stable equilibrium solution is introduced, see figure 2.9.

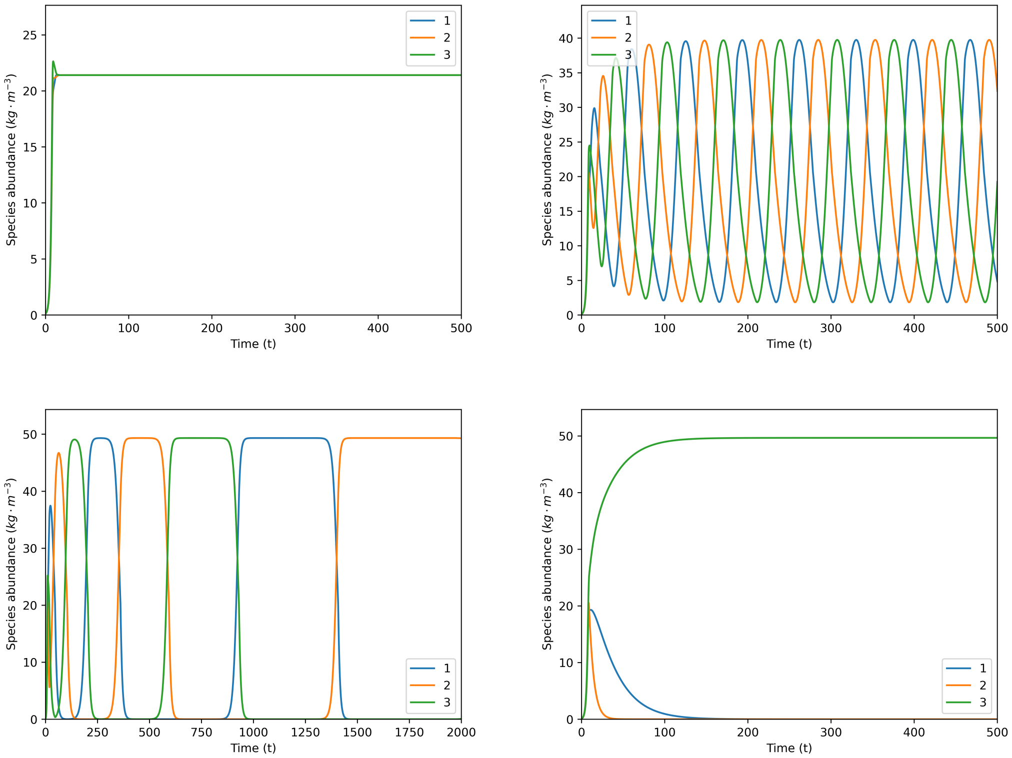

Figure 2.9: The values describing the species abundances over time. The upper left and right graph have α respectively equal to 0.2 and 0.4. The lower left and right graph have α respectively set to 0.6 and 1.1.

It is apparent that the coexistence of the species is limited when $\alpha < 0.25$ or $\alpha > 1.00$. However, in the range $0.25 < a < 1.00$ either a limit cycle can emerge, which has a constant frequency, or a heteroclinic cycle can emerge, which has a gradually decreasing frequency over time (Palacios, 2007). This implies that the period of a heteroclinic cycle gets infinitely long, but the cyclic behaviour never stops. The graph belonging to $\alpha = 0.4$ describes a heteroclinic cycle. Another property of heteroclinic cycles is that they oscillate between equilibrium solutions. The system, where $\alpha = 0.4$, has three unstable equilibrium solutions where $N_i = \frac{148}{3}$, for a single $i \in \{1, 2, 3\}$, and the other two plankton species are extinct. It can be seen that the system cycles through these unstable equilibrium solutions. In turn the plankton species get close to one equilibrium solution, without intersecting it, and converging to another equilibrium solution.

While a heteroclinic cycle is mathematically valid behaviour, it does not imply a physically realistic system. Plankton species cannot get infinitesimally close to extinction without becoming extinct due to the plankton population being discretized. However, the figures above do imply that when a heteroclinic cycle is found, it is possible to alter certain system parameters that changes the heteroclinic cycle into a limit cycle, which are physically realistic due to no species present in a limit cycle growing infinitesimally small.

2.4.3. 3 resource types and 4 plankton species

The third example describes a system with three resource types and four plankton species. The parameters describing this system are:

D	0.25
S_1	6
S_2	10
S_3	14
m_1	0.25
m_2	0.25
m_3	0.25
m_4	0.25
r_1	1.00
r_2	1.00
r_3	1.00
r_4	1.00

$$K = \begin{bmatrix} 1.00 & 0.90 & 0.30 & 1.04 \\ 0.30 & 1.00 & 0.90 & 0.71 \\ 0.90 & 0.30 & 1.00 & 0.46 \end{bmatrix}$$

$$c = \begin{bmatrix} 0.04 & 0.07 & 0.04 & 0.10 \\ 0.08 & 0.08 & 0.10 & 0.10 \\ 0.14 & 0.10 & 0.10 & 0.16 \end{bmatrix}$$

$$R_{init} = \begin{bmatrix} R_1 & R_2 & R_3 \end{bmatrix} = \begin{bmatrix} 6 & 10 & 14 \end{bmatrix}$$

$$N_{init} = \begin{bmatrix} N_1 & N_2 & N_3 & N_4 \end{bmatrix} = \begin{bmatrix} 0.11 & 0.12 & 0.13 & 0.10 \end{bmatrix}$$

Plankton species N_1, N_2, N_3 are introduced to the system at $t = 0$, plankton species N_4 is instantly homogeneously introduced to the system at $t = 1000$. It is emphasized that introducing the new species does not change the existence of any previously established equilibrium solutions where the new species was extinct. This results in a simulation where the four plankton species eventually coexist on three resource types, see figure 2.10.

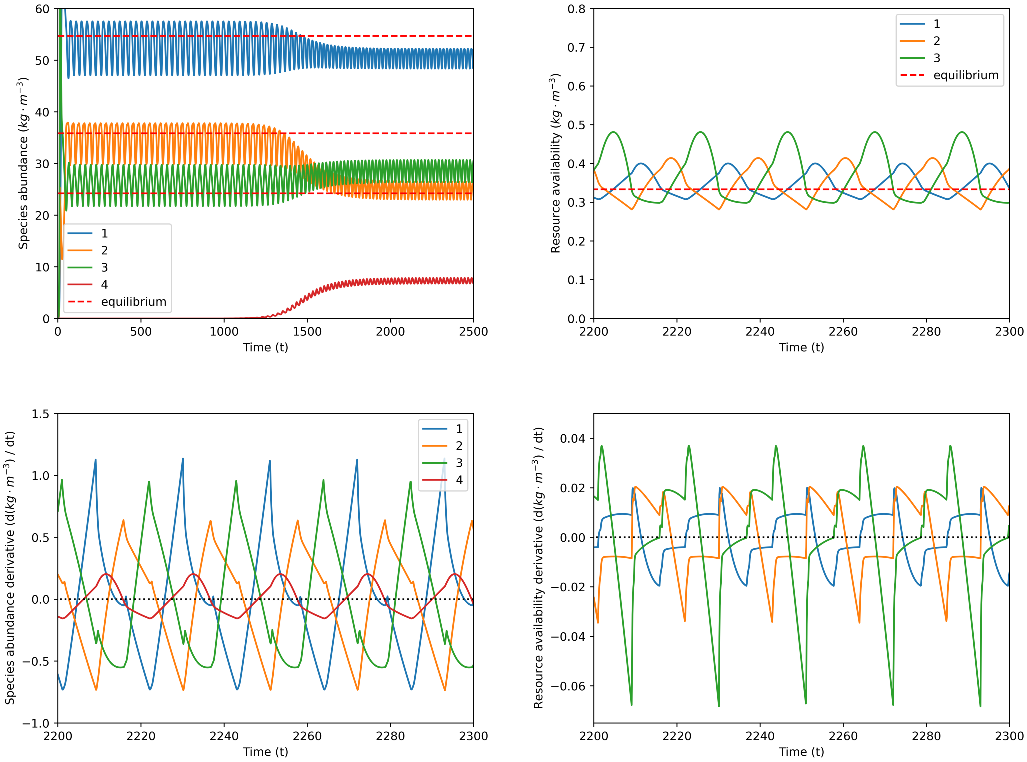

Figure 2.10: The values describing the species abundance and the resource availability over time, the respective derivatives are plotted below.

The equilibrium solution that the plankton species oscillate around, before the fourth plankton species is introduced, is equal to:

$$\begin{bmatrix} N_1 & N_2 & N_3 & N_4 \end{bmatrix} = \begin{bmatrix} 54.717, & 35.849 & 24.214 & 0.000 \end{bmatrix}$$

$$\begin{bmatrix} R_1 & R_2 & R_3 \end{bmatrix} = \begin{bmatrix} 0.333 & 0.333 & 0.333 \end{bmatrix}$$

Plotting the phase diagrams, see figure 2.11, gives insight into the new limit cycles that appear when the fourth plankton species is introduced.

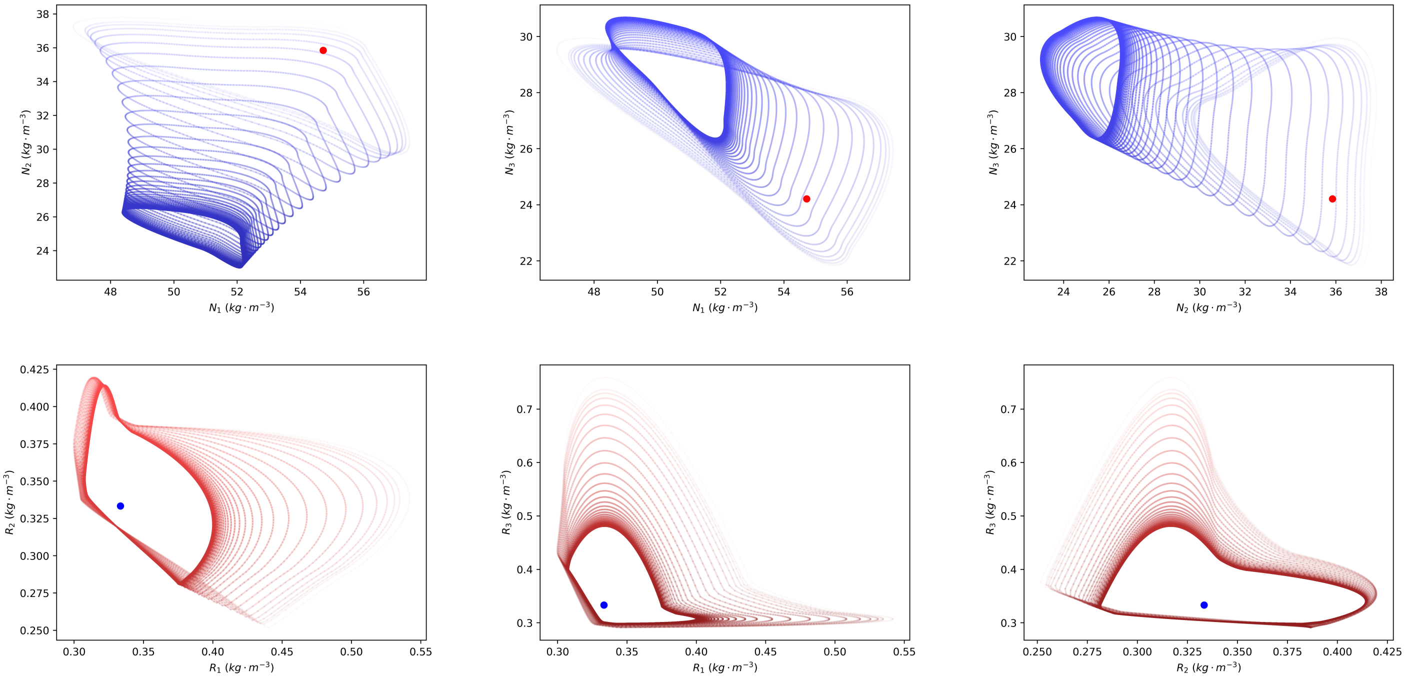

Figure 2.11: Phase diagrams representing how the plankton species and resource types approach a new limit cycle over time.

Observe how the new orthogonal projections of the limit cycles for the plankton species do not contain the previous equilibrium solution. In contrast, the new orthogonal projections of the limit cycles for the resource types do contain the previous equilibrium solution.

Most importantly, the paradox of plankton is present in this example. It is shown that four plankton species are able to coexist on three resource types. Therefore it is possible to achieve more biodiversity than previously expected based on the principle of competitive exclusion.

2.4.4. 3 resource types and 5 plankton species

In this example it is shown that five plankton species can coexist on three resource types. The same system as in the previous example is used. However, at $t = 2000$ a new plankton species is added to the model that can coexist with the previously present species, the values for which can be found in the appendix. It is also shown that, for the coexistence of these five species, it is not required for the pre-existing plankton species to closely follow the limit cycle created by N_1, N_2, N_3 before introducing the new plankton species N_4 and N_5. This is done by introducing all the species at $t = 0$. The results of these simulations can be seen in figure 2.12.

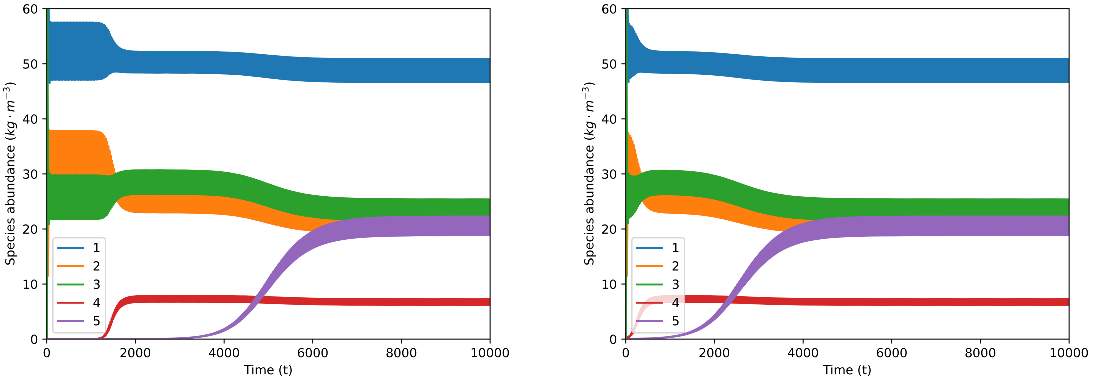

Figure 2.12: The values describing the species abundance over time. In the left graph the new species N_4 and N_5 are added at respectively $t = 1000$ and $t = 2000$. In the right graph all the plankton species N_1, N_2, N_3, N_4, N_5 are simultaneously added at $t = 0$.

Furthermore, a slight variation in the parameters describing plankton species N_5 is made, $c_{35} = 0.20$, that allows for a single asymptotically stable equilibrium solution to exist:

$$\begin{bmatrix} N_1 & N_2 & N_3 & N_4 & N_5 \end{bmatrix} = \begin{bmatrix} 0.000 & 65.764 & 0.000 & 0.000 & 36.552 \end{bmatrix}$$

$$\begin{bmatrix} R_1 & R_2 & R_3 \end{bmatrix} = \begin{bmatrix} 0.300 & 2.911 & 0.113 \end{bmatrix}$$

In figure 2.13, it is shown that introducing this altered plankton species N_5^* makes the system converge to this new equilibrium solution and erases the previously achieved biodiversity.

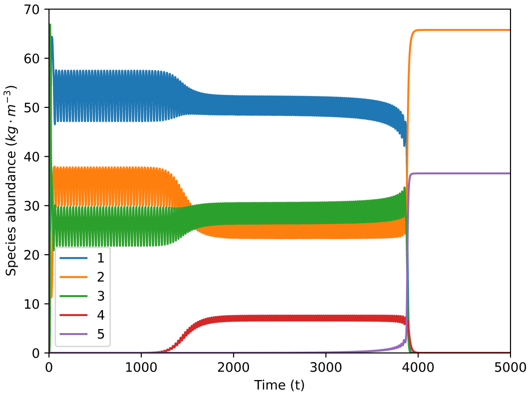

Figure 2.13: The values describing the species abundance over time. At $t = 2000$ plankton species N_5^* is introduced, it can be seen that the limit cycles disappear and plankton species N_1, N_2, N_4 go extinct.

Furthermore, in section (2.2.6), it was shown that in an equilibrium solution there can never coexist more plankton species than resource types. Therefore, by introducing this altered species N_5^* it is possible to predict, even before running the simulation, that at a minimum two plankton species will go extinct.

2.4.5. 3 resource types and 9 plankton species

There exist examples where nine plankton species are coexisting on three resource types, see figure 2.14.

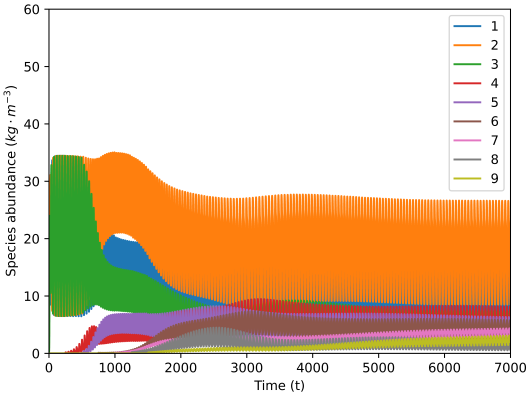

Figure 2.14: The values describing the species abundance over time. The plankton species N_1, N_2, N_3 are introduced with the respective initial values $0.11, 0.12, 0.13$. The plankton species $N_4, N_5, ..., N_9$ are all introduced with an initial value of 0.10.

Interestingly, the introduction of the sixth plankton species N_6 introduces an asymptotically stable equilibrium solution to the system:

$$\begin{bmatrix} N_1 & N_2 & N_3 & N_4 & N_5 & N_6 & N_7 & N_8 & N_9 \end{bmatrix}$$
$$= \begin{bmatrix} 0.000 & 0.000 & 17.303 & 0.000 & 0.000 & 17.970 & 0.000 & 0.000 & 0.000 \end{bmatrix}$$
$$\begin{bmatrix} R_1 & R_2 & R_3 \end{bmatrix} = \begin{bmatrix} 0.217 & 0.250 & 4.676 \end{bmatrix}$$

Which usually erases the coexistence of the previously present species. However, it is observed that the system manages to avoid intersecting with the region where the plankton species and resource types converge to this asymptotically stable equilibrium.

This is an indicator of how the coexistence of these plankton species is more fragile. Where previously, for five plankton species, it was possible to introduce them all simultaneously to the system, due to there being no need of avoiding a region of convergence. Now the system's biodiversity is significantly dependent on the initial conditions of the system. Changing the initial value of N_6 from 0.100 to 0.025 allows the system to coincide with the region of convergence to the asymptotically stable equilibrium solution, and erases the previously achieved biodiversity, as shown in figure 2.15.

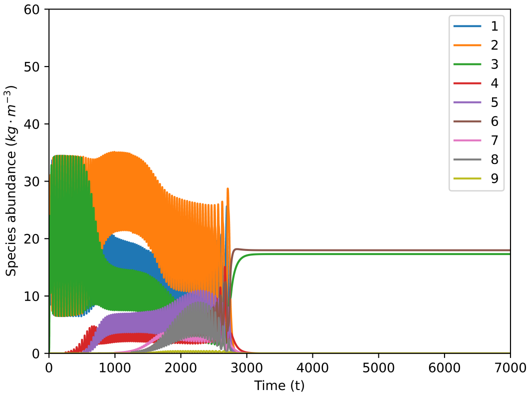

Figure 2.15: The values describing the species abundance over time. The plankton species N_1, N_2, N_3 are introduced with the respective initial values $0.11, 0.12, 0.13$. The plankton species N_4, N_5, N_7, N_8, N_9 are all introduced with an initial value of 0.10. N_6 is introduced with an initial value of 0.025.

2.5. Coexistence of plankton species

In the previous sections several examples of the paradox of plankton were demonstrated. It was shown that it is possible for plankton species to coexist in a system with k resource types and $n > k$ plankton species. However, this seems unintuitive due to the principle of competitive exclusion. Which states that, in equilibrium, no more plankton species can coexist than the resource types available. The important insight is to realize that this principle is only true for equilibrium solutions. As long as plankton species and resource types avoid converging to an equilibrium solution the coexistence of the plankton species is not limited by the amount of resource types in the system. This provides an explanation to the paradox of plankton. (A graphical intuition is given in figure (2.11).) However, this does imply that the paradox only appears when certain conditions are met. In this section these specific conditions will be analyzed.

Firstly, it was shown in the previous examples that a system with any asymptotically stable equilibrium solutions, that have a region of convergence equal to the domain of the system, will eventually satisfy the principle of competitive exclusion. Therefore, it is required, for the paradox of plankton to occur, that the plankton species and resource types avoids converging to any equilibrium solution. Asymptotically stable equilibrium solutions act as attractors, unstable equilibrium solutions act as repellors. Thus, it is concluded that a necessary, but not sufficient, condition to prevent converging to an equilibrium solution is that all the equilibrium solutions of the system need to be unstable.

There exist exceptions to this rule, for example in the system with nine plankton species and three resource types it was shown that the convergence to a asymptotically stable equilibrium can be avoided by not intersecting with its region of convergence. However, this makes the coexistence of multiple plankton species more fragile, because additional precautions needs to be taken to avoid intersecting with this region. Furthermore, in the following sections it will be assumed that any asymptotically stable equilibrium solution will have a region of convergence equal to the domain of the system.

A plankton species will be regarded as dominant if it introduces an asymptotically stable equilibrium solution to a system, with a region of convergence equal to the domain of the system. Therefore it is possible to state that introducing a dominant plankton species to a system will remove any previously achieved biodiversity where more plankton species are present than the amount of resource types.

Analyzing the stability of an equilibrium solution uses the eigenvalues of the Jacobian associated with that solution as described in section (2.3.1). Finding explicit conditions for when an equilibrium solution is asymptotically stable or unstable gets more challenging once more plankton species and resource types are added to the system due to the size of the Jacobian increasing. In this section a simplified system will be introduced which simplifies the linear stability analysis. Then using this simplification it will be proven that an asymptotically stable equilibrium solution will always be present in a simplified system with one plankton species and one resource type and in a simplified system with two plankton species and two resource types.

By further analyzing this simplified system, it will be shown that the plankton species and resource types are bounded above. This prevents any variable from going to infinity when there are only unstable equilibrium solutions present. Additionally, due to the physical constraints of the model it is clear that all the plankton species and resource types are bounded below by zero. By stating that the system is bounded it is possible to use an analog of the Poincare-Bendixson theorem to provide additional parameter constraints for the coexistence of plankton species. In section (2.2.4) it also was shown that, in a system with n plankton species, there always exists a trivial equilibrium solution where $N_i = 0$ for all $i \in \{1, 2, ..., n\}$. Using the simplified model allows one to find conditions for which this trivial solution is unstable.

2.5.1. Conservation of mass

An important principle to be able to analyze the model further is the conservation of mass. However, due to the resources flowing out of the chemostat model while plankton stay inside the container the mass of each respective resource is not always conserved in the model. Thankfully, a condition exists which guarantees that mass is conserved. To find this condition imagine a system with n plankton species and k resource types. Note that the time derivative of plankton species (2.2) can be inserted into the time derivative of resource types (2.3) to find for all $j \in \{1, 2, ..., k\}$:

$$\frac{dR_j(t)}{dt} = D(S_j - R_j(t)) - \sum_{i=1}^{n} c_{ji}\frac{dN_i(t)}{dt} - \sum_{i=1}^{n} c_{ji}m_iN_i(t)$$

Solving for S_j and using the linearity of the derivative gives:

$$S_j = \frac{1}{D}\frac{d}{dt}(R_j(t) + \sum_{i=1}^{n} c_{ji}N_i(t)) + R_j(t) + \frac{1}{D}\sum_{i=1}^{n} c_{ji}m_iN_i(t)$$

Now the assumption is made that all the plankton species have a mortality rate equal to the system's turnover rate: $m_i = D$ for all $i \in \{1, 2, ..., n\}$. By introducing the temporary function $f(t) = R_j(t) + \sum_{i=1}^{n} c_{ji}N_i(t)$ it can be seen that:

$$S_j = \frac{1}{D}\frac{df(t)}{dt} + f(t)$$

Solving this ordinary differential equation yields:

$$f(t) = S_j + C \cdot e^{-\frac{t}{D}} \tag{2.19}$$

The presence of the negative exponential term is to account for the initial conditions of the model. The finite constant C can be determined with these conditions: $C = f(0) - S_j = R_j(0) + \sum_{i=1}^{n} c_{ji}N_i(0) - S_j$. Typically the initial conditions are chosen such that $R_j(0) = S_j$, which further negates the influence of this term. Furthermore, as time increases the negative exponential factor will approach 0, due to the turnover rate D being strictly positive. Combining these insights allows one to formally state that if $m_i = D$, for all $i \in \{1, 2, ..., n\}$, it holds true that, for all $j \in \{1, 2, ..., k\}$, mass is conserved by the following equation:

$$R_j(t) + \sum_{i=1}^{n} c_{ji}N_i(t) = S_j$$

This equation allows one to significantly reduce the model by eliminating the R_j variables:

$$\frac{dN_i}{dt} = N_i(\boldsymbol{\mu_i}(S_1 - \sum_{i=1}^{n} c_{1i}N_i, S_2 - \sum_{i=1}^{n} c_{2i}N_i, ..., S_k - \sum_{i=1}^{n} c_{ki}N_i) - m_i)$$

$$\Downarrow$$

$$\frac{dN_i}{dt} = N_i(r_i(1 - max(\frac{K_{1i}}{K_{1i} + S_1 - \sum_{i=1}^{n} c_{1i}N_i}, \frac{K_{2i}}{K_{2i} + S_2 - \sum_{i=1}^{n} c_{2i}N_i}, ..., \frac{K_{ki}}{K_{ki} + S_k - \sum_{i=1}^{n} c_{ki}N_i})) - m_i)$$

This simplified model does not exactly reproduce the behaviour of the previous model, which includes resources, due to it not accounting for the initial conditions. However, all the previous examples can be reproduced with this simplified model. Furthermore, because this simplified model becomes more accurate as time progresses, it can be used to analyze the local behaviour of equilibrium solutions.

2.5.2. Resources and plankton species are bounded

Using the conservation of mass principle, it can be proven that resources and plankton species are bounded at any time t. The system from the previous section is used. State that, for any $t \in [0, \infty)$, $R_j(t) \geq 0$ and $N_i(t) \geq 0$ and examine equation (2.19) to find:

$$0 \leq R_j(t) \leq S_j + C \cdot e^{-\frac{t}{D}}$$

$$0 \leq \sum_{i=1}^{n} c_{ji}N_i(t) \leq S_j + C \cdot e^{-\frac{t}{D}}$$

The initial conditions determine the value of C, which has to satisfy $-S_j \leq C$ for a bounded solution to exist. Inserting the expression for C gives:

$$0 \leq R_j(0) + \sum_{i=1}^{n} c_{ji}N_i(0)$$

This condition is always satisfied due to $0 \leq R_j(t)$ and $0 \leq N_i(t)$ for any $t \in [0, \infty)$. Therefore, it follows that R_j and N_i do not go to infinity as $t \to \infty$. This concludes the proof that resources and plankton species are bounded if $D = m_i$ for all $i \in \{1, 2, ..., n\}$.

2.5.3. Poincare-Bendixson theorem

Approaching the problem from a statistical view yields more insights. Firstly, introduce the expectation operator:

$$\mathbb{E}\{f(t)\} = \lim_{\boldsymbol{t^*} \to \infty} \frac{1}{\boldsymbol{t^*}} \int_0^{\boldsymbol{t^*}} f(t)dt$$

This allows one to state the following analog of the Poincare-Bendixson theorem (Levins, 1979):
If $f(t)$ is a bounded function in some domain, then:

$$\mathbb{E}\{\frac{df(t)}{dt}\} = 0$$

This can be shown by using the fundamental theorem of calculus and the fact that boundedness implies a constant upper and lower bound:

$$\int_0^{\boldsymbol{t^*}} \frac{df(t)}{dt}dt = f(\boldsymbol{t^*}) - f(0) \leq max(f(t)) - min(f(t))$$

$$\Downarrow$$

$$\mathbb{E}\{\frac{df(t)}{dt}\} = \lim_{\boldsymbol{t^*} \to \infty} \frac{max(f(t)) - min(f(t))}{\boldsymbol{t^*}} = 0$$

This is equivalent with stating that if a function $f(t)$ is bounded, then the area $\int_0^\infty \frac{df(t)}{dt}dt = 0$. Because in the examples given in the previous section the plankton species and resources were bounded this can be motivated graphically by inspecting the derivatives given in figures (2.6) and (2.10).

A consequence of this statement is that for the original ordinary differential equations (2.2) describing the species abundance, where it is desired that in equilibrium $N_i > 0$ for all $i \in \{1, 2, ..., n\}$, the following has to be true:

$$0 = \mathbb{E}\{\frac{dN_i}{dt}\frac{1}{N_i}\} = \mathbb{E}\{\boldsymbol{\mu_i}(R_1, R_2, ..., R_k) - m_i\}$$

$$\Downarrow$$

$$\frac{m_i}{r_i} = \mathbb{E}\{min(\frac{R_1}{K_{1i} + R_1}, \frac{R_2}{K_{2i} + R_2}, ..., \frac{R_k}{K_{ki} + R_k})\} < min(\frac{1}{\frac{K_{1i}}{S_1} + 1}, \frac{1}{\frac{K_{2i}}{S_2} + 1}, ..., \frac{1}{\frac{K_{ki}}{S_k} + 1})$$

Here the conservation of mass principle is used to find that $R_j < S_j$ for all $j \in \{1, 2, ..., k\}$. These insights give a condition that determines if coexistence via sustained motion is **not** possible:

$$\exists i \in \{1, 2, ..., n\} \; ; \; \frac{m_i}{r_i} \geq min(\frac{S_1}{K_{1i} + S_1}, \frac{S_2}{K_{2i} + S_2}, ..., \frac{S_k}{K_{ki} + S_k}) \tag{2.20}$$

Intuitively this condition can be understood by realizing that coexistence of all the plankton species is more unlikely if one of the species is insufficiently nourished by the resources available in the system. One way in which a species can be malnourished is if it has a relatively large mortality rate m_i in comparison to its optimal growth rate r_i, or if its half saturation constants K_{ji} are too large in comparison to the supply of resources in the system S_j. This condition can also be rewritten as:

$$\forall i \in \{1, 2, ..., n\} \; ; \; max(\frac{K_{1i}}{S_1}, \frac{K_{2i}}{S_2}, ..., \frac{K_{ki}}{S_k}) < \frac{r_i - m_i}{m_i}$$

This can be seen as a consequence of Liebig's law of the minimum, the health of a plankton species is determined by the resource it is most poorly dependent on. In sections (2.4.2) and (2.4.3) it can be seen how the system's parameters satisfy this constraint.

2.6. Conditions for unstable equilibrium solutions

In this section linear stability analysis will be used to determine whether it is possible to obtain systems with only unstable equilibrium solutions. Firstly, it will be determined when the trivial equilibrium solution is unstable. Secondly, a system with one plankton species and one resource type will be analyzed. Thirdly, a system with two plankton species and two resource types will be analyzed. For this system, a proof will be given that an asymptotically stable equilibrium solution always exist if the two plankton species are allowed to coexist in equilibrium.

2.6.1. Stability of the trivial equilibrium solution

As proven in section (2.2.4) a system with k resource types and n plankton species always has a trivial equilibrium solution where $N_i = 0$ and $R_j = S_j$ for $\forall i \in \{1,2,...,n\}; \forall j \in \{1,2,...,k\};$. Analyzing the stability of this equilibrium solution in the simplified model yields that for all $i \in \{1,2,...,n\}$ there exists a $j \in \{1,2,...,k\}$ such that:

$$\frac{\partial}{\partial N_i}(\frac{dN_i}{dt}) = r_i(1 - \frac{K_{ji}}{S_j + K_{ji}}) - m_i$$

$$\forall \boldsymbol{i^*} \in \{1,2,...,n\} \neq i\ ;\ \ \frac{\partial}{\partial N_{\boldsymbol{i^*}}}(\frac{dN_i}{dt}) = 0;$$

Due to these derivatives the Jacobian is a diagonal matrix, which implies that the eigenvalues are equal to the diagonal elements of the Jacobian. Therefore, the trivial equilibrium solution is unstable if:

$$\exists i \in \{1,2,...,n\};\ \frac{\partial}{\partial N_i}(\frac{dN_i}{dt}) > 0$$

This is equivalent with stating that:

$$\exists i \in \{1,2,...,n\}\ ;\ min(\frac{K_{1i}}{S_1}, \frac{K_{2i}}{S_2}, ..., \frac{K_{ki}}{S_k}) < \frac{r_i - m_i}{m_i}$$

Notice the similarity with inequality (2.20). However, that inequality checks if the weakest plankton species can exist in the system. This inequality instead checks if there is at least one plankton species that is capable of sustaining itself with the best resources available for that species. In all the examples shown so far this inequality has been satisfied.

2.6.2. 1 resource type and 1 plankton species

The simplified model for a system with one plankton species and one resource type where $m_1 = D$ is:

$$\frac{dN_1}{dt} = N_1(r_1(1 - \frac{K_{11}}{K_{11} + S_1 - c_{11}N_1}) - m_1)$$

Finding the equilibrium solution for $N_1 > 0$ by setting $\frac{dN_1}{dt} = 0$ yields:

$$N_1 = \frac{1}{c_{11}}(S_1 - K_{11}\frac{m_1}{r_1 - m_1})$$

The Jacobian is given by:

$$J = \left[\tfrac{\partial}{\partial N_1}(\tfrac{dN_1}{dt})\right] = \left[r_1 \cdot (1 - \tfrac{K_{11}}{S_1 + K_{11} - c_{11}N_1} - \tfrac{K_{11}c_{11}N_1}{(S_1 + K_{11} - c_{11}N_1)^2}) - m_1\right] = \lambda$$

Inserting the found equilibrium value for N_1, and using that $m_1 < r_1$ and $0 < N_1$, shows that the eigenvalue λ is always negative:

$$\lambda = -r_1 \frac{S_1 - K_{11}\frac{m_1}{r_1 - m_1}}{(\frac{r_1}{r_1 - m_1})^2} < 0$$

As a consequence, the equilibrium solution is always asymptotically stable. This also shows that this eigenvalue does not have any imaginary component. Therefore, no oscillatory behaviour is expected for a system with one plankton species and one resource type.

Furthermore, imagine a system with one resource type and two plankton species. There exist two equilibrium solutions, in each of them one of the two plankton species is extinct. By definition, one of the plankton species will be more efficient at consuming the resource than the other species. In the long run this causes the other plankton species to go extinct and the system approaches a stable monoculture equilibrium (Huisman Weissing, 1999).

2.6.3. 2 resource types and 2 plankton species

In this section a proof will be given that in a system with two resource types and two plankton species, where $m_1 = m_2 = D$, there always exists an asymptotically stable equilibrium solution, if the two plankton species can coexist in equilibrium. In this system there are two main types of equilibrium solutions. One where a single plankton species is extinct and one where no plankton species are extinct. Several conditions will be analyzed which determines the existence and stability of these equilibrium solutions.

Start with ordinary differential equations describing the system's plankton species N_1, N_2:

$$\frac{dN_1}{dt} = N_1(r_1(1 - max(\frac{K_{11}}{K_{11} + S_1 - c_{11}N_1 - c_{12}N_2}, \frac{K_{21}}{K_{21} + S_2 - c_{21}N_1 - c_{22}N_2})) - m_1) \tag{2.21}$$

$$\frac{dN_2}{dt} = N_2(r_2(1 - max(\frac{K_{12}}{K_{12} + S_1 - c_{11}N_1 - c_{12}N_2}, \frac{K_{22}}{K_{22} + S_2 - c_{21}N_1 - c_{22}N_2})) - m_2) \tag{2.22}$$

The assumption is made that, in the first equilibrium analyzed, the first species N_1 relies on the K_{11}-factor, and the second species N_2 relies on the K_{22}-factor. The only other combination possible, as motivated in section (2.2.5), is that N_1 depends on the K_{21}-factor and N_2 depends on the K_{12}-factor. The assumption leads to an analog of the minimization condition that was seen before which will be called the maximization conditions:

$$\frac{K_{11}}{K_{11} + S_1 - c_{11}N_1 - c_{12}N_2} \geq \frac{K_{21}}{K_{21} + S_2 - c_{21}N_1 - c_{22}N_2} \tag{2.23}$$

$$\frac{K_{12}}{K_{12} + S_1 - c_{11}N_1 - c_{12}N_2} \leq \frac{K_{22}}{K_{22} + S_2 - c_{21}N_1 - c_{22}N_2} \tag{2.24}$$

These assumptions allows one to eliminate the maximization function from the model:

$$\frac{dN_1}{dt} = N_1(r_1(1 - \frac{K_{11}}{K_{11} + S_1 - c_{11}N_1 - c_{12}N_2}) - m_1)$$

$$\frac{dN_2}{dt} = N_2(r_2(1 - \frac{K_{22}}{K_{22} + S_2 - c_{21}N_1 - c_{22}N_2}) - m_2)$$

The equilibrium solution can be found by setting $\frac{dN_1}{dt} = 0$ and $\frac{dN_2}{dt} = 0$ and by assuming that $N_1 > 0$, $N_2 > 0$. These conditions give the equations:

$$S_1 - \frac{m_1 K_{11}}{r_1 - m_1} = c_{11}N_1 + c_{12}N_2 \geq 0 \tag{2.25}$$

$$S_2 - \frac{m_2 K_{22}}{r_2 - m_2} = c_{21}N_1 + c_{22}N_2 \geq 0 \tag{2.26}$$

Note that these are identical to equation (2.12) where $q_1 = 1$ and $q_2 = 2$. Thus the simplified model will give the same equilibrium solutions as the original model. Solving for N_1 and N_2 gives:

$$N_1 = \frac{c_{22}(S_1 - \frac{m_1 K_{11}}{r_1 - m_1}) - c_{12}(S_2 - \frac{m_2 K_{22}}{r_2 - m_2})}{c_{11}c_{22} - c_{12}c_{21}} \tag{2.27}$$

$$N_2 = \frac{c_{11}(S_2 - \frac{m_2 K_{22}}{r_2 - m_2}) - c_{21}(S_1 - \frac{m_1 K_{11}}{r_1 - m_1})}{c_{11}c_{22} - c_{12}c_{21}} \tag{2.28}$$

Furthermore, by inserting equations (2.25-2.26) the inequalities (2.23-2.24) can be respectively rewritten as:

$$\frac{K_{21}}{r_1 - m_1} \leq \frac{K_{22}}{r_2 - m_2} \tag{2.29}$$

$$\frac{K_{12}}{r_2 - m_2} \leq \frac{K_{11}}{r_1 - m_1} \tag{2.30}$$

For the other equilibrium solution, where N_1 relies on the K_{21}-factor and N_2 relies on the K_{12} factor, the maximization conditions are:

$$\frac{K_{11}}{K_{11} + S_1 - c_{11}N_1 - c_{12}N_2} \leq \frac{K_{21}}{K_{21} + S_2 - c_{21}N_1 - c_{22}N_2}$$

$$\frac{K_{12}}{K_{12} + S_1 - c_{11}N_1 - c_{12}N_2} \geq \frac{K_{22}}{K_{22} + S_2 - c_{21}N_1 - c_{22}N_2}$$

By following similar steps as before, it is found that these conditions can be rewritten as:

$$\frac{K_{12}}{r_2 - m_2} \geq \frac{K_{11}}{r_1 - m_1} \tag{2.31}$$

$$\frac{K_{21}}{r_1 - m_1} \geq \frac{K_{22}}{r_2 - m_2} \tag{2.32}$$

Note that inequality (2.29) and (2.32) cannot both be true at the same time. This implies that for a system with two plankton species and two resource type there only exists one single equilibrium solution where $N_1, N_2 > 0$.

Reconsidering the equilibrium solution given in equations (2.27-2.28). Because N_1 and N_2 are bounded, as proven in section (2.5.2), this equilibrium solution only exists if $c_{11}c_{22} \neq c_{12}c_{21}$. These values for N_1 and N_2 will be inserted in the Jacobian for this system:

$$J = \begin{bmatrix} \frac{\partial}{\partial N_1}(\frac{dN_1}{dt}) & \frac{\partial}{\partial N_2}(\frac{dN_1}{dt}) \\ \frac{\partial}{\partial N_1}(\frac{dN_2}{dt}) & \frac{\partial}{\partial N_2}(\frac{dN_2}{dt}) \end{bmatrix}$$

Where the derivatives are equal to:

$$\frac{\partial}{\partial N_1}(\frac{dN_1}{dt}) = r_1 \cdot (1 - \frac{K_{11}}{S_1 + K_{11} - c_{11}N_1 - c_{12}N_2} - \frac{K_{11}c_{11}N_1}{(S_1 + K_{11} - c_{11}N_1 - c_{12}N_2)^2}) - m_1$$

$$\frac{\partial}{\partial N_2}(\frac{dN_2}{dt}) = r_2 \cdot (1 - \frac{K_{22}}{S_2 + K_{22} - c_{21}N_1 - c_{22}N_2} - \frac{K_{22}c_{22}N_2}{(S_2 + K_{22} - c_{21}N_1 - c_{22}N_2)^2}) - m_2$$

$$\frac{\partial}{\partial N_2}(\frac{dN_1}{dt}) = -r_1 \cdot \frac{K_{11}c_{12}N_1}{(S_1 + K_{11} - c_{11}N_1 - c_{12}N_2)^2}$$

$$\frac{\partial}{\partial N_1}(\frac{dN_2}{dt}) = -r_2 \cdot \frac{K_{22}c_{21}N_2}{(S_2 + K_{22} - c_{21}N_1 - c_{22}N_2)^2}$$

Reinserting equation (2.25) and (2.26) and using the assumption that all the variables used are strictly positive and that $m_1 < r_1$, $m_2 < r_2$ gives:

$$\frac{\partial}{\partial N_1}(\frac{dN_1}{dt}) = -r_1(1 - \frac{m_1}{r_1})^2 \frac{c_{11}N_1}{K_{11}} < 0$$

$$\frac{\partial}{\partial N_2}(\frac{dN_2}{dt}) = -r_2(1 - \frac{m_2}{r_2})^2 \frac{c_{22}N_2}{K_{22}} < 0$$

$$\frac{\partial}{\partial N_2}(\frac{dN_1}{dt}) = -r_1 \cdot (1 - \frac{m_1}{r_1})^2 \frac{c_{12}N_1}{K_{11}} < 0$$

$$\frac{\partial}{\partial N_1}(\frac{dN_2}{dt}) = -r_2 \cdot (1 - \frac{m_2}{r_2})^2 \frac{c_{21}N_2}{K_{22}} < 0$$

The eigenvalues of the Jacobian can be expressed as: $\lambda_{1,2} = \frac{1}{2}(tr(J) \pm \sqrt{tr(J)^2 - 4\,det(J)})$. For a unstable equilibrium it is required that $\lambda_1 > 0$ or $\lambda_2 > 0$, which is equivalent with stating that $tr(J) + \sqrt{tr(J)^2 - 4\,det(J)} > 0$. Because $tr(J) < 0$ it follows that if $det(J) < 0$ then there exists at least one positive eigenvalue:

$$det(J) < 0 \Leftrightarrow c_{11}c_{22} < c_{12}c_{21} \tag{2.33}$$

This condition allows an unstable equilibrium solution to exist where both plankton species are non-extinct. Furthermore, this condition can be inserted into the positivity conditions $N_1 > 0,\ N_2 > 0$ (2.27-2.28) to find:

$$c_{22}(S_1 - \frac{m_1K_{11}}{r_1 - m_1}) < c_{12}(S_2 - \frac{m_2K_{22}}{r_2 - m_2}) \tag{2.34}$$

$$c_{11}(S_2 - \frac{m_2K_{22}}{r_2 - m_2}) < c_{21}(S_1 - \frac{m_1K_{11}}{r_1 - m_1}) \tag{2.35}$$

However, this does not mean that all the equilibrium solution of this system are unstable as well. Consider the other potential equilibrium solutions where one of the two plankton species is extinct. These can be found by setting $\frac{dN_i}{dt} = 0$ and $N_{\boldsymbol{i^*}} = 0$, where $i \neq \boldsymbol{i^*}$, and solving for N_i:

$$(N_1, N_2) = \begin{cases} (\frac{1}{c_{11}}(S_1 - \frac{m_1K_{11}}{r_1-m_1}), 0) \\ (\frac{1}{c_{21}}(S_2 - \frac{m_1K_{21}}{r_1-m_1}), 0) \\ (0, \frac{1}{c_{22}}(S_2 - \frac{m_2K_{22}}{r_2-m_2})) \\ (0, \frac{1}{c_{12}}(S_1 - \frac{m_2K_{12}}{r_2-m_2})) \end{cases} \tag{2.36}$$

Note that the positivity conditions $N_1 \geq 0,\ N_2 \geq 0$ are satisfied in every equilibrium solution by using equations (2.25-2.26) and (2.29-2.30):

$$S_2 - \frac{m_1K_{21}}{r_1 - m_1} \geq S_2 - \frac{m_2K_{22}}{r_2 - m_2} > 0$$

$$S_1 - \frac{m_2K_{12}}{r_2 - m_2} \geq S_1 - \frac{m_1K_{11}}{r_1 - m_1} > 0$$

Furthermore, the first and second equilibrium solution each have one respective maximization condition:

$$\frac{K_{11}}{K_{11} + S_1 - c_{11}N_1 - c_{12}N_2} \geq \frac{K_{21}}{K_{21} + S_2 - c_{21}N_1 - c_{22}N_2} \tag{2.37}$$

$$\frac{K_{11}}{K_{11} + S_1 - c_{11}N_1 - c_{12}N_2} \leq \frac{K_{21}}{K_{21} + S_2 - c_{21}N_1 - c_{22}N_2} \tag{2.38}$$

Rewriting these conditions and inserting each respective equilibrium solution gives:

$$c_{11}(S_2 - \frac{m_1K_{21}}{r_1 - m_1}) \geq c_{21}(S_1 - \frac{m_1K_{11}}{r_1 - m_1}) \tag{2.39}$$

$$c_{11}(S_2 - \frac{m_1K_{21}}{r_1 - m_1}) \leq c_{21}(S_1 - \frac{m_1K_{11}}{r_1 - m_1}) \tag{2.40}$$

Note that only one of these two inequalities can be true, which shows that only the maximization condition of the first or second equilibrium solution can be satisfied. Additionally, this implies that due to symmetry only one maximization condition of either the third or fourth equilibrium solution can be satisfied as well. This proves that if there exists an equilibrium solution where $N_1 > 0$ and $N_2 > 0$, then there always exists an equilibrium solution where $N_1 > 0$ and $N_2 = 0$ and another equilibrium solution where $N_1 = 0$ and $N_2 > 0$.

To analyze the stability of the equilibrium solutions (2.36), where $N_2 = 0$, the Jacobian will be constructed. The derivatives used in the Jacobian, where $j = 1$ for the first equilibrium solution and $j = 2$ for the second equilibrium solution and $\boldsymbol{j^*} \in \{1, 2\}$, are:

$$\frac{\partial}{\partial N_1}(\frac{dN_1}{dt}) = r_1 \cdot (1 - \frac{K_{j1}}{S_j + K_{j1} - c_{j1}N_1 - c_{j2}N_2} - \frac{K_{j1}c_{j1}N_1}{(S_j + K_{j1} - c_{j1}N_1 - c_{j2}N_2)^2}) - m_1 \tag{2.41}$$

$$\frac{\partial}{\partial N_2}(\frac{dN_2}{dt}) = r_2 \cdot (1 - \frac{K_{\boldsymbol{j^*}2}}{S_{\boldsymbol{j^*}} + K_{\boldsymbol{j^*}2} - c_{\boldsymbol{j^*}1}N_1 - c_{\boldsymbol{j^*}2}N_2} - \frac{K_{\boldsymbol{j^*}2}c_{\boldsymbol{j^*}2}N_2}{(S_{\boldsymbol{j^*}} + K_{\boldsymbol{j^*}2} - c_{\boldsymbol{j^*}1}N_1 - c_{\boldsymbol{j^*}2}N_2)^2}) - m_2 \tag{2.42}$$

$$\frac{\partial}{\partial N_2}(\frac{dN_1}{dt}) = -r_1 \cdot \frac{K_{j1}c_{j2}N_1}{(S_j + K_{j1} - c_{j1}N_1 - c_{j2}N_2)^2} \tag{2.43}$$

$$\frac{\partial}{\partial N_1}(\frac{dN_2}{dt}) = -r_2 \cdot \frac{K_{\boldsymbol{j^*}2}c_{\boldsymbol{j^*}1}N_2}{(S_{\boldsymbol{j^*}} + K_{\boldsymbol{j^*}2} - c_{\boldsymbol{j^*}1}N_1 - c_{\boldsymbol{j^*}2}N_2)^2} \tag{2.44}$$

As an example, by setting $\boldsymbol{j^*} = 1$ it is implied that N_2 will depend on the K_{12}-factor of (2.22) when the system deviates slightly from $N_2 = 0$. However, the actual index $\boldsymbol{j^*}$ is arbitrary because it is infeasible to predict which specific resource the second plankton species N_2 will most depend on. Inserting the equilibrium solutions $(N_1, N_2) = (\frac{1}{c_{j1}}(S_j - \frac{m_1 K_{j1}}{r_1 - m_1}), 0)$ and rewriting these derivatives gives:

$$\frac{\partial}{\partial N_1}(\frac{dN_1}{dt}) = -r_1 \cdot (1 - \frac{m_1}{r_1})^2 \frac{c_{j1}N_1}{K_{j1}}$$

$$\frac{\partial}{\partial N_2}(\frac{dN_2}{dt}) = r_2 \cdot (1 - \frac{K_{\boldsymbol{j^*}2}}{S_{\boldsymbol{j^*}} + K_{\boldsymbol{j^*}2} - c_{\boldsymbol{j^*}1}N_1}) - m_2$$

$$\frac{\partial}{\partial N_2}(\frac{dN_1}{dt}) = -r_1 \cdot (1 - \frac{m_1}{r_1})^2 \frac{c_{j2}N_1}{K_{j1}}$$

$$\frac{\partial}{\partial N_1}(\frac{dN_2}{dt}) = 0$$

Once again using the eigenvalue identity $\lambda_{1,2} = \frac{1}{2}(tr(J) \pm \sqrt{tr(J)^2 - 4\,det(J)})$ and the motivation given previously, shows that if $tr(J) + \sqrt{tr(J)^2 - 4\,det(J)} < 0$ then the equilibrium solution is asymptotically stable. Because $\frac{\partial}{\partial N_1}(\frac{dN_1}{dt}) < 0$ and $\frac{\partial}{\partial N_1}(\frac{dN_2}{dt}) = 0$, the condition can be simplified. This allows one to state that an asymptotically stable equilibrium solution is present if:

$$\frac{\partial}{\partial N_2}(\frac{dN_2}{dt}) < 0$$

Inserting the equilibrium solutions, where $N_2 = 0$, and rewriting this condition gives:

$$c_{j1}(S_{\boldsymbol{j^*}} - \frac{m_2 K_{\boldsymbol{j^*}2}}{r_2 - m_2}) < c_{\boldsymbol{j^*}1}(S_j - \frac{m_1 K_{j1}}{r_1 - m_1}) \tag{2.45}$$

Each combination of indices $j, \boldsymbol{j^*} \in \{1, 2\}$ will be considered separately. Firstly, the condition is satisfied when $j = \boldsymbol{j^*} = 2$ due to inequality (2.29). Secondly, the condition is not satisfied when $j = \boldsymbol{j^*} = 1$ due to inequality (2.30). Thirdly, the condition is satisfied when $j = 1$ and $\boldsymbol{j^*} = 2$ due to inequality (2.35). Finally, the condition is not satisfied when $j = 2$ and $\boldsymbol{j^*} = 1$ due to it not satisfying the maximization condition of N_1 (2.40):

$$c_{21}(S_1 - \frac{m_1 K_{11}}{r_1 - m_1}) < c_{21}(S_1 - \frac{m_2 K_{12}}{r_2 - m_2}) < c_{11}(S_2 - \frac{m_1 K_{21}}{r_1 - m_1}) \tag{2.46}$$

However, the equilibrium solution is not valid when $j = 2$ and $\boldsymbol{j^*} = 1$ due to the maximization condition of N_2:

$$\frac{K_{12}}{K_{12} + S_1 - c_{11}N_1 - c_{12}N_2} \geq \frac{K_{22}}{K_{22} + S_2 - c_{21}N_1 - c_{22}N_2}$$

It is allowed to simply use the equilibrium condition to analyze if this inequality is satisfied, when a small deviation is made from the equilibrium solution, because it is assumed that the resource targeted by the species does not change for a small deviation (2.17). Rewrite this condition and insert the equilibrium solution to find:

$$S_1 - \frac{K_{12}K_{21}}{K_{22}} \frac{m_1}{r_1 - m_1} \leq \frac{c_{11}}{c_{21}}(S_2 - \frac{m_1 K_{21}}{r_1 - m_1})$$

Use inequality (2.29) to see that:

$$\frac{K_{21}}{K_{22}} \frac{r_2 - m_2}{r_1 - m_1} < 1$$

Then use inequality (2.30) to state:

$$S_1 - \frac{K_{12}K_{21}}{K_{22}} \frac{m_1}{r_1 - m_1} = S_1 - \frac{K_{21}}{K_{22}} \frac{r_2 - m_2}{r_1 - m_1} \frac{m_2 K_{12}}{r_2 - m_2} \geq S_1 - \frac{m_2 K_{12}}{r_2 - m_2} \geq S_1 - \frac{m_1 K_{11}}{r_1 - m_1}$$

This implies that to satisfy the maximization condition for N_2 it is required that:

$$c_{21}(S_1 - \frac{m_1 K_{11}}{r_1 - m_1}) \leq c_{11}(S_2 - \frac{m_1 K_{21}}{r_1 - m_1})$$

However, this can never be satisfied due to the maximization condition for N_1 when $j = 2$ (2.40). Thus it is not possible to satisfy both maximization conditions for N_2 and N_1 when $j = 2$ and $\boldsymbol{j^*} = 1$.

Now the only issue remaining is the case where $j = \boldsymbol{j^*} = 1$ because the equilibrium is also unstable for those indices. This will be counteracted with an example for the first equilibrium solution of (2.36). It will be shown that it is not possible to satisfy the maximization condition for N_2 when $j = \boldsymbol{j^*} = 1$:

$$\frac{K_{12}}{K_{12} + S_1 - c_{11}N_1 - c_{12}N_2} \geq \frac{K_{22}}{K_{22} + S_2 - c_{21}N_1 - c_{22}N_2}$$

The first step is to rewrite this condition and insert the equilibrium solution:

$$S_2 - \frac{K_{11}K_{22}}{K_{12}} \frac{m_1}{r_1 - m_1} \leq \frac{c_{21}}{c_{11}}(S_1 - \frac{m_1 K_{11}}{r_1 - m_1})$$

Then use the inequality (2.35) to find that:

$$(S_2 - \frac{m_2 K_{22}}{r_2 - m_2}) \leq \frac{c_{21}}{c_{11}}(S_1 - \frac{m_1 K_{11}}{r_1 - m_1})$$

One then finds that:

$$S_2 - \frac{K_{11}K_{22}}{K_{12}} \frac{m_1}{r_1 - m_1} \geq (S_2 - \frac{m_2 K_{22}}{r_2 - m_2}) \Leftrightarrow \frac{K_{11}}{r_1 - m_1} \leq \frac{K_{12}}{r_2 - m_2} \tag{2.47}$$

However, it follows that this inequality is never satisfied due to inequality (2.30). This implies that it is not possible to satisfy the maximization condition of N_2 when $j = \boldsymbol{j^*} = 1$.

To conclude, for any of the allowed combinations of $j,\ \boldsymbol{j^*}$ where there exists a valid equilibrium solution, here $j = \boldsymbol{j^*} = 1$ and $j = 2$, $\boldsymbol{j^*} = 1$ are not valid as shown previously, it holds that there is at least one asymptotically stable equilibrium solution where $N_1 > 0$ and $N_2 = 0$.

Furthermore, if there exists an equilibrium solution where $N_1 > 0$ and $N_2 > 0$ and there is one unstable equilibrium solutions where one of the two plankton species is extinct, then the equilibrium solution where $N_1 > 0$ and $N_2 > 0$ must be asymptotically stable.

For there to be one unstable equilibrium solution with one extinct plankton species, it is required that $j = 1$ and $\boldsymbol{j^*} = 2$. This implies that inequality (2.35) is not satisfied, which implies that the equilibrium solution where no plankton species are extinct must be asymptotically stable. The other possible values combinations of $j,\ \boldsymbol{j^*} \in \{1, 2\}$ are not possible because the existence and asymptotic stability of those equilibrium solutions, where one of the two species is extinct, solely depends on the existence of an equilibrium solution where $N_1 > 0$ and $N_2 > 0$, regardless of whether its asymptotically stable or unstable.

Repeating all the steps (2.37-2.47) for the equilibrium solutions (2.36) where $N_1 = 0$ yields the same results due to the symmetry of the equilibrium solutions. Furthermore, repeating all the steps (2.23-2.47) for the equilibrium solution where N_1 depends on the K_{21}-factor and N_2 depends on the K_{12}-factor also gives the same results. This is due to the symmetry in the inequalities and equilibrium solutions that were found, an example is (2.29-2.30) versus (2.31-2.32).

This finishes the proof which states that, in a system with two plankton species and two resource types, if there is one equilibrium solution where $N_1 > 0$ and $N_2 > 0$ then there exists at least one asymptotically stable equilibrium.

Finally, if no equilibrium solution exists where $N_1 > 0$ and $N_2 > 0$ then there always exists an asymptotically stable equilibrium solution. If, in the equilibrium solution, the two plankton species are dependent on the same resource, one of the two species will go extinct, as motivated in the previous section. If, in the equilibrium solution, the species are dependent on separate resources, no coexistence is possible between the two species due to no equilibrium solution with $N_1 > 0$ and $N_2 > 0$ being present, therefore it is also expected that one of the two plankton species will eventually dominate over the other. Both these situations causes an asymptotically stable monoculture equilibrium solution to appear, where the weaker species has gone extinct.

Therefore, in a simplified system with two resource types and two plankton species an asymptotically stable equilibrium solution is always present, which prevents the paradox of plankton from appearing. It is concluded that a minimum of three resource types must be present in a simplified system to be able to disobey the principle of competitive exclusion.

3

Expanding the model

The current model contains several interesting phenomena: limit cycles, asymptotically stable equilibrium solutions, and the paradox of plankton. In this chapter the model will be expanded to put it in a more realistic context. Light intensity will be considered as an additional food resource for every plankton species. Furthermore, the model will be put in the physical context of a river with dispersive and advective mass transfer to analyze the behaviour of the model in a more realistic context than the bare chemostat model. The goal is to gain more insight into what parameters and conditions causes the paradox of plankton to appear for these more realistic models.

3.1. Disregarding Liebig's law of the minimum

When deciding how to expand the existing model, it is beneficial to analyze the shortcomings of the current model. Firstly, in biological systems it is observed that Liebig's law of the minimum is not always satisfied. For example, there are plankton species for which the growth rate depends on the combination of iron and nitrogen, instead of the minimum of these two resources (Tilman, 1982). An alternative to Liebig's law is letting the actual growth rate of a plankton species i, when there are simultaneously k unique amounts of resources present, be defined as:

$$\mu_i(R_1, R_2, ..., R_k) = \prod_{j=1}^{k} \mu_i(R_j) = \prod_{j=1}^{k} \frac{r_i R_j}{K_{ji} + R_j} \tag{3.1}$$

Using this new definition, combinations of plankton species and resource types can still be found that generate limit cycles (Huisman & Weissing, 2002b). In figure 3.1, a limit cycle of three species coexisting on three resource types can be observed.

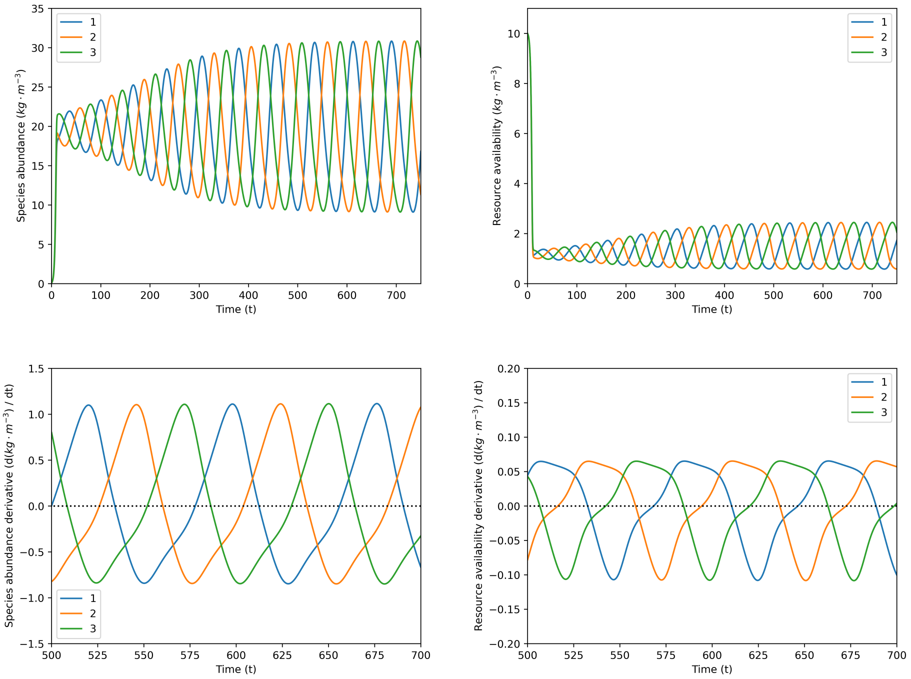

Figure 3.1: The values describing the species abundance and the resource availability over time, the respective derivatives are plotted below. Note how these are continuously differentiable due to the absence of the minimization function in the model. The specific values for this system are in the appendix.

Additionally, systems of species and resources can be found that disprove the principle of competitive exclusion. For example, when a limit cycle is present with three oscillating plankton species, it is possible for a fourth species to be introduced in the system and coexist with the already present plankton species, as shown in figure 3.2.

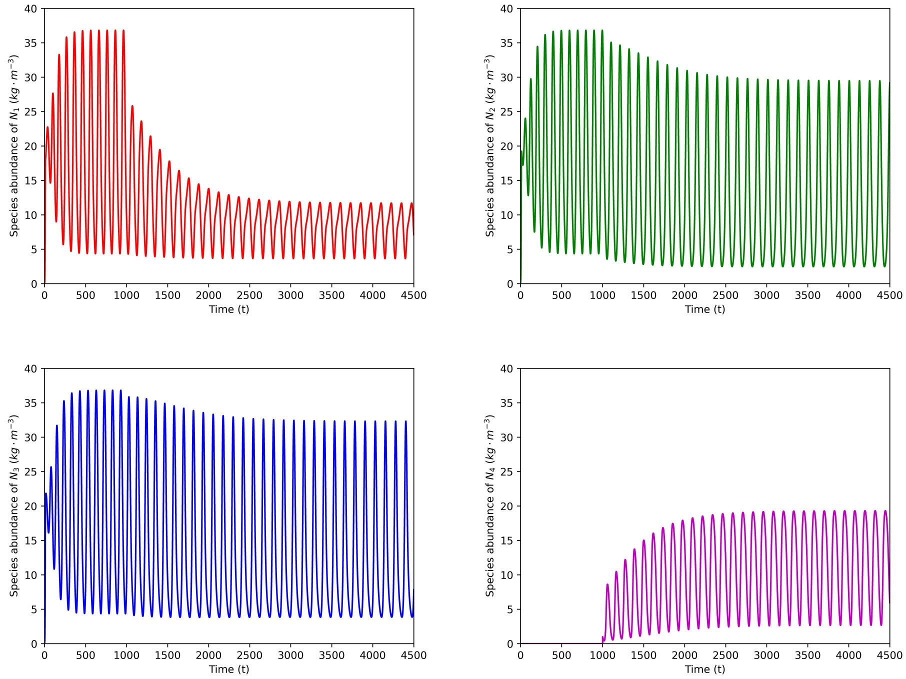

Figure 3.2: Four different species coexisting on three resource types, while disregarding Liebig's law of the minimum.

However, completely disregarding Liebig's law of the minimum is biologically inaccurate. There are plankton species where the growth rate depends on the presence of two other resource types, but not where it depends on ten other resource types. The choice is made to partly disregard Liebig's law up to two resource types, instead of all the resource types present.

Combining what has been observed so far, imagine a system with three plankton species and three resource types. The first and third species, N_1 and N_3, behave the same as in the original situation, only depending on each individual resource type. However, for the second species N_2 there are two resource types, R_1 and R_3, such that the growth rate depends on the combination of the resource types instead of the individual resource types. The following definitions for the growth rates of the plankton species can then be constructed:

$$\begin{aligned} \mu_1(R_1,R_2,R_3) &= min(\mu_1(R_1),\mu_1(R_2),\mu_1(R_3)) \\ \mu_2(R_1,R_2,R_3) &= min(\mu_2(R_1)\cdot\mu_2(R_3),\mu_2(R_2)) \\ \mu_3(R_1,R_2,R_3) &= min(\mu_3(R_1),\mu_3(R_2),\mu_3(R_3)) \end{aligned} \tag{3.2}$$

3.2. Introducing depth and light intensity

A frequently analyzed problem is how plankton grow under different lighting conditions. Each plankton species absorbs light in order to grow. However, when the concentration of plankton gets higher the light intensity decreases due to there being more light-absorbing material. As a result the growth rate of the plankton species decreases. When the concentration decreases the light intensity increases, with an increase in the growth rate for the plankton species as a result (Huisman et al., 2002a). This dynamic has the same behaviour as a limit cycle, therefore it is beneficial to observe the effect of light intensity in the model to see how it potentially enables a more bio-diverse ecosystem.

To be able to incorporate the effect of light intensity fully into the model, depth z is added as a spatial dimension. According to Lambert-Beer's law, light absorption is proportional (i.e., the change of light intensity with depth) is proportional to the concentrations of the light-absorbing substances and to the local light intensity (Huisman et al., 2002a):

$$\frac{\partial I}{\partial z}(z,t) = -(H_{bg} + \sum_{i=1}^{n} h_i^{'}\frac{N_i(t)}{V})I(z,t) \tag{3.3}$$

Here, a summation is done over all the light-absorbing plankton species concentrations, where V is the volume of the chemostat system, $h_i^{'}$ is a proportionality constant equivalent with the specific light attenuation coefficient of plankton species i. A new proportionality constant $h_i = h_i^{'}\frac{1}{V}$ is introduced so the volume does not have to be directly accounted for.The background turbidity H_{bg} is a constant indicating the clarity of the fluid that is contained in the system when there are no plankton species present. A higher background turbidity indicates a murkier fluid, completely clear fluid has no background turbidity. For readability define the following time dependent function:

$$\omega(t) = H_{bg} + \sum_{i=1}^{n} h_i N_i(t) > 0 \tag{3.4}$$

Solving the ordinary differential equation yields an explicit expression for the light intensity at a specific depth z and time t:

$$I(z,t) = I_{in}\cdot e^{-\omega(t)z} \tag{3.5}$$

The factor I_{in} describes the light intensity incident upon the surface of the volume in the chemostat model. It can be seen that the light intensity decreases exponentially with depth. The specific growth rate of a plankton species i as a function of light intensity at a specific time and depth can be modelled by the Monod equation [10]:

$$\boldsymbol{\xi}_i(z,t) = \frac{r_i I(z,t)}{L_i + I(z,t)} \tag{3.6}$$

Here L_i is the half-saturation constant and r_i is the growth rate under ideal circumstances. Do note that there are other relations possible besides the Monod equation. However, due to its earlier usage in the chemostat model it will be used here. Assume that the system has a finite depth $Z > 0$. Because it is assumed that the chemostat model is well mixed, the growth rate of a plankton species depends on the average value of $\boldsymbol{\xi}_i(z,t)$ over the entire depth of the system. This can be expressed as:

$$\overline{\boldsymbol{\xi}_i(t)} = \frac{1}{Z}\int_0^Z \boldsymbol{\xi}_i(z,t)dz = \frac{r_i}{Z\omega(t)} ln(\frac{L_i + I_{in}}{L_i + I_{in}e^{-Z\omega(t)}}) \tag{3.7}$$

A graph of the growth parameter against the weighted sum of plankton species $\omega(t)$ is shown in figure 3.3.

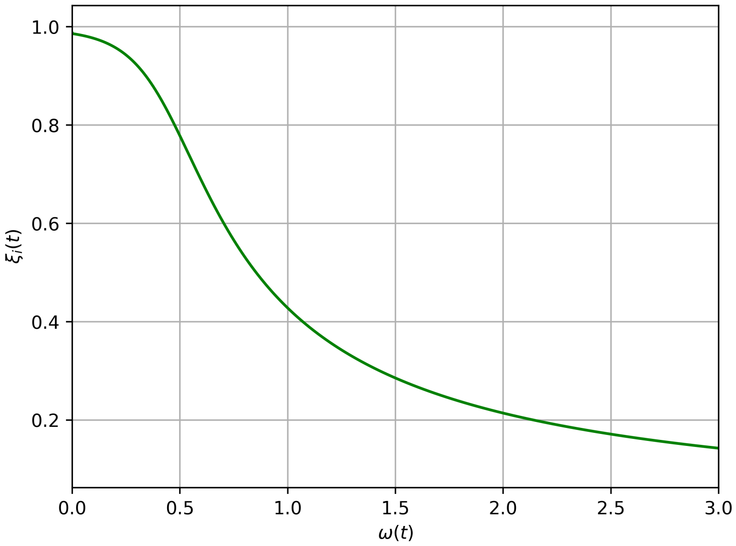

Figure 3.3: The growth parameter $\overline{\boldsymbol{\xi}_i(t)}$ plotted against the weighted sum of plankton species $\omega(t)$. The parameters are $Z = 10;\ L_i = 0.07;\ I_{in} = 5;\ r_i = 1$. It is observed how the growth parameter changes rapidly in $\omega(t) \leq 2.0$. Furthermore, note how in equation (3.7) the depth Z has the same influence as $\omega(t)$.

It can be argued that the growth rate of a plankton species always depends on the light intensity, in addition to food resource with the minimal growth rate determined by equation (2.1). In the previous section it was motivated how important behaviour, such as the existence of limit cycles and the paradox of plankton, still occurs when more than one food resource, as the strict version of Liebig's law dictates, is considered to determine the actual growth rate.

Adding light intensity to the model should give more insight into the paradox of plankton. Due to the light intensity having a negative exponential dependency on the total amount of plankton present in the system (3.5), while the growth rate of individual plankton species depends positively on the light intensity (3.6). One can hypothesize that this dynamic shares characteristics with an oscillating spring, due to there always being a restoring force to some balance point. The expectation is therefore to observe more oscillatory behaviour when adding light intensity to the model. Due to the paradox of plankton depending on the existence of a limit cycle, it is expected to observe more biodiverse systems when including light intensity in the model.

Having laid down the groundwork, it is possible to formulate this expansion of the model formally. The definition of the model's growth rate $\boldsymbol{\mu}_i(R_1, R_2, ..., R_k)$ is changed to:

$$\boldsymbol{\mu}_i(R_1, R_2, ..., R_k, N_1, N_2, ..., N_n) = min(\frac{r_iR_1}{K_{1i}+R_1}, ..., \frac{r_iR_k}{K_{ki}+R_k}) \cdot \frac{r_i}{Z\omega(t)} ln(\frac{L_i + I_{in}}{L_i + I_{in}e^{-Z\omega(t)}}) \tag{3.8}$$

Where the definition of $\omega(t)$ is given in equation (3.4).

Simulating a system with four plankton species and three resource types, it is observed that the paradox of plankton still holds true, even when light intensity is added to the model.. The system's parameters are the same parameters as in section (2.4.3) with the addition of:

I_{in}	2.5
H_{bg}	0.01

$$\begin{bmatrix} L_1 & L_2 & L_3 & L_4 \end{bmatrix} = \begin{bmatrix} 0.01 & 0.01 & 0.01 & 0.01 \end{bmatrix}$$

$$\begin{bmatrix} h_1 & h_2 & h_3 & h_4 \end{bmatrix} = \begin{bmatrix} 0.01 & 0.01 & 0.01 & 0.01 \end{bmatrix}$$

Furthermore, in figure 3.4, it is also observed that the stability of the coexistence of the four species significantly depends on the depth of the system.

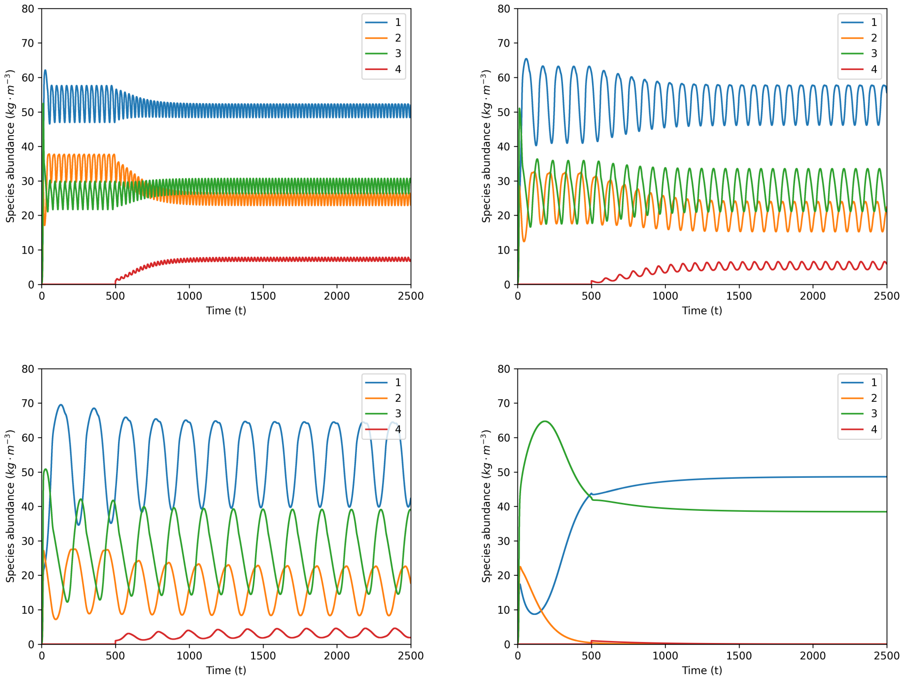

Figure 3.4: The top left graph uses a depth of $1\ m$, the top right graph uses a depth of $7.5\ m$, the bottom left graph uses a depth of $10\ m$ and the bottom right graph uses a depth of $15\ m$. It can be seen how the limit cycle has a higher frequency and lower amplitude in more shallow environments. If the environment is too deep it can be seen that a coexistence of four species can not be maintained and two species go extinct.

In other simulations, not shown, it was found that any change in parameters that significantly increases the value of $\xi_i(t)$, which in turn increases the frequency and decreases the amplitude of the limit cycle, (3.7) allows for the coexistence of more plankton species. For example, if the system is a deep lake with murky water more biodiversity can be achieved by introducing plankton species that have small h_i values, they absorb little light, and by increasing the light intensity I_{in} that is incident on the surface of the lake.

Additionally, seasonality can be modelled by varying the light intensity over time. During the summer period the sun will shine for more hours thus there will be more light intensity on average, the opposite occurs during the winter period. This characteristic can be modelled by introducing:

$$I_{in}(t) = 0.81 + 0.4 \cdot sin(t\frac{2\pi}{365}) \tag{3.9}$$

The simulation of the model with this added seasonal characteristic is shown in figure 3.5.

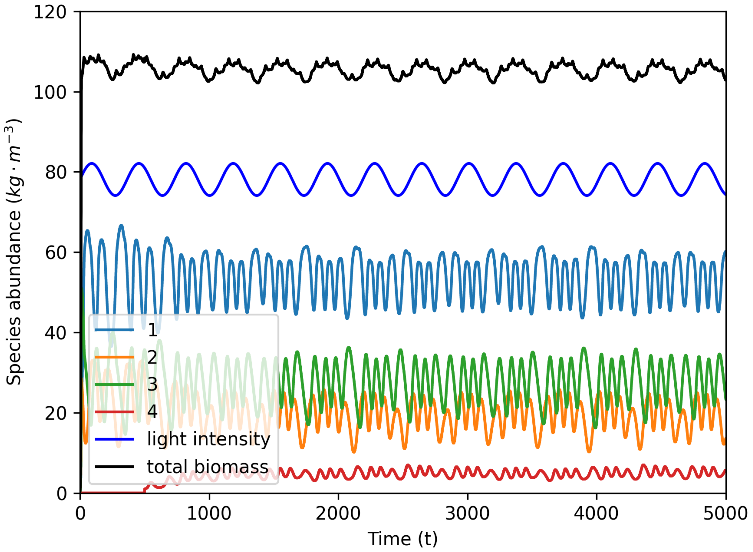

Figure 3.5: The species abundance of every plankton species over time. The depth Z is set to $7.5m$. The light intensity shown in this graph is a scaled up representation version of the actual light intensity (3.9). This is done to more easily compare the fluctuations in the light intensity to other fluctuations in the simulation.

Firstly, it is observed that the period and amplitude of the cycle describing the plankton species increases as the light intensity decreases, and vice versa. Secondly, a notable influence of this included seasonality is that the total biomass of the system increases as the light intensity increases. In a system with a constant light intensity the total biomass remains constant, but in this system the total biomass grows and shrinks according to the light intensity. This increase in total biomass during the summer period, and decrease during the winter period, is also observed in experiments tracking phytoplankton biomass in the Southern Ocean (Arteaga et al., 2020).

3.3. Introducing a spatial context with dispersion and advection

To further expand the model, the context of a river, over x, with finite length $\mathcal{L}$ $[m]$ and a varying depth $Z(x)$ $[m]$ will be added. Furthermore, it will be assumed that plankton move around in the river in a dispersive manner, locations with a high density of plankton will spread out to places with a lower density, determined by the dispersion constant $\mathcal{D}$ $[m^2s^{-1}]$. Secondly, it is assumed that there is a laminar flow present in the river, which creates advective mass transfer. Taking mass starting at $x = 0$ to $x = \mathcal{L}$ by advection, the laminar flow is characterized by the flow speed v $[m\, s^{-1}]$. The next step is to derive the ordinary differential equation that describes the change of a substance in the river over time.

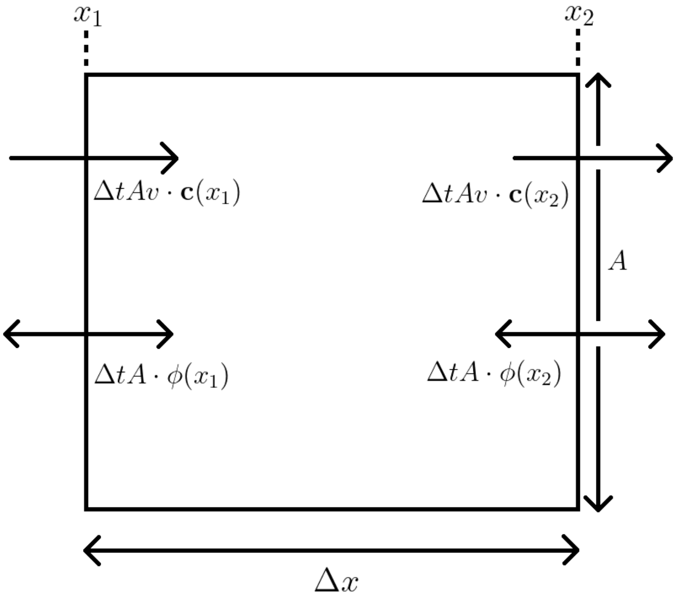

Figure 3.6: A schematic overview of the change of a concentration $\mathbf{c}(x)$ over some time interval Δt, due to dispersive and advective mass transfer, in a small fragment of length Δx.

From this river analyze a small fragment ranging from x_1 to x_2, see figure 3.6. Imagine that the river has a constant depth D_r and width W_r. Introduce the variable $\Delta x = x_2 - x_1$. Furthermore, the river has a concentration $\boldsymbol{c}(x)$ of a substance that varies over the length of the river. The change of this concentration $\boldsymbol{c}(x)$ over a small time period Δt is analyzed. Firstly account for the advective mass transfer for this small fragment, at the left side of this fragment $\Delta t A v \cdot \boldsymbol{c}(x_1)$ enters the fragment, at the right side of this fragment $\Delta t A v \cdot \boldsymbol{c}(x_2)$ leaves the system, where $A = D_r W_r$. Secondly account for the dispersive mass transfer for this small fragment, to enable this introduce the dispersive flux $\phi(x)$ $[kg \cdot m^{-2}]$ which is the amount of substance that flows through an unit area. It is assumed that a positive mass flux goes from left to right. At the left side of the fragment $\Delta t A \cdot \phi(x_1)$ of mass enters or leaves the fragment, at the right side $\Delta t A \cdot \phi(x_2)$ of mass leaves the fragment. Analyzing the change of mass over time for this small volume $V = \Delta x D_r W_r$:

$$V \Delta \boldsymbol{c} = in_{adv} - out_{adv} + in_{dis} - out_{dis} \tag{3.10}$$

$$= \Delta t A v \cdot \boldsymbol{c}(x_1) - \Delta t A v \cdot \boldsymbol{c}(x_2) + \Delta t A \cdot \phi(x_1) - \Delta t A \cdot \phi(x_2)$$

Using Fick's law $\psi = -D\frac{dc}{dx}$ (Mudde, 1998), which relates the diffusive flux to the derivative of the concentration of the substance , assuming $\mathcal{D}$ is constant, and letting $\Delta t \to 0$; $\Delta x \to 0$ allows one to state that:

$$\frac{\Delta \boldsymbol{c}}{\Delta t} = -v\frac{(\boldsymbol{c}(x_2) - \boldsymbol{c}(x_1))}{\Delta x} - \frac{\psi(x_1) - \psi(x_2)}{\Delta x} \Rightarrow \frac{\partial \boldsymbol{c}}{\partial t} = -\frac{\partial \psi}{\partial x} - v\frac{\partial \boldsymbol{c}}{\partial x} = D\frac{\partial^2 \boldsymbol{c}}{\partial x^2} - v\frac{\partial \boldsymbol{c}}{\partial x} \tag{3.11}$$

Modelling this behaviour in the model does imply that the influence of the turnover variable D, in the original model (2.2-2.3), is not accounted for, because its behaviour is replaced by the flow speed v.

Furthermore, the depth of the river varies over the length of the river according to the equation $Z(x)$. However, this does influence the flow speed of the river v. Imagine a river with a constant width W and varying depth $Z(x)$ and varying flow speed $v(x)$ for $0 \leq x \leq \mathcal{L}$. The advective volumetric flux of the river is assumed to be constant: $\frac{d}{dx}(W \cdot Z(x) \cdot v(x)) = 0$. This implies that:

$$v(x) = \frac{Z(0)}{Z(x)} \cdot v(0) \tag{3.12}$$

(In all sections except (3.4.5) it is assumed that the depth is constant $Z(x) = Z$, which implies that the flow speed $v(x) = v$ is constant as well.)

Expanding the model, with n plankton species and k resource types, to incorporate these dispersive and advective mass transfer phenomena gives:

$$\frac{\partial N_i}{\partial t} = N_i(\boldsymbol{\mu_i}(R_1, R_2, ..., R_k) - m_i) + \mathcal{D}\frac{\partial^2 N_i}{\partial x^2} - v(x)\frac{\partial N_i}{\partial x} \tag{3.13}$$

$$\frac{\partial R_j}{\partial t} = -\sum_{i=1}^{n} c_{ji} N_i \boldsymbol{\mu_i}(R_1, R_2, ..., R_k) + \mathcal{D}\frac{\partial^2 R_j}{\partial x^2} - v(x)\frac{\partial R_j}{\partial x} \tag{3.14}$$

The boundary conditions are chosen such that the modified model still shares characteristics with the original chemostat model. One of these is that the resources flow into the system at a steady rate with a given concentration S_j. This can be included in the model by virtue of the boundary conditions:

$$N_i(t, 0) = 0 \tag{3.15}$$

$$N_i(t, \mathcal{L}) = 0 \tag{3.16}$$

$$R_j(t, 0) = S_j \tag{3.17}$$

$$R_j(t, \mathcal{L}) = 0 \tag{3.18}$$

And initial conditions:

$$N_i(0, x) = f_i(x) \tag{3.19}$$

$$R_j(0, x) = g_j(x) \tag{3.20}$$

To be able to numerically simulate these partial differential equations, the finite-difference method will be used for the spatial and temporal dimension (Vuik, 2015). Split the spatial dimension into $\mathcal{N} + 1$ equal segments, such that for any $\boldsymbol{i} \in \{0, 1, 2, ..., \mathcal{N}\}$:

$$x = \boldsymbol{i}\frac{\mathcal{L}}{\mathcal{N}} = \boldsymbol{i}\Delta x \tag{3.21}$$

The values of $N_i(t, x), R_j(t, x)$, where $i \in \{1, 2, ..., n\}$ and $j \in \{1, 2, ..., k\}$ will only be defined on these discrete x values defined in equation (3.21). Furthermore, introduce the shorthand notation $N_i^{(m)} = N_i(t, m\Delta x)$ and $R_j^{(m)} = R_j(t, m\Delta x)$. Inserting these discrete x values into equation (3.13) and (3.14) and using the central difference approximation, for all $0 \neq x \neq \mathcal{L}$, yields that for any $m \in \{1, 2, ..., \mathcal{N} - 2, \mathcal{N} - 1\}$:

$$\frac{\partial N_i^{(m)}}{\partial t} = N_i^{(m)}(\boldsymbol{\mu_i}(R_1^{(m)}, R_2^{(m)}, ..., R_k^{(m)}) - m_i) + \mathcal{D}\frac{N_i^{(m+1)} - 2N_i^{(m)} + N_i^{(m-1)}}{\Delta x^2} - v(m\Delta x)\frac{N_i^{(m+1)} - N_i^{(m-1)}}{2\Delta x} \tag{3.22}$$

$$\frac{\partial R_j^{(m)}}{\partial t} = -\sum_{i=1}^{n} c_{ji} N_i^{(m)} \boldsymbol{\mu_i}(R_1^{(m)}, R_2^{(m)}, ..., R_k^{(m)}) + \mathcal{D}\frac{R_j^{(m+1)} - 2R_j^{(m)} + R_j^{(m-1)}}{\Delta x^2} - v(m\Delta x)\frac{R_j^{(m+1)} - R_j^{(m-1)}}{2\Delta x} \tag{3.23}$$

Due to the boundary conditions, $N_i^{(0)} = N_i^{(\mathcal{N})} = R_j^{(\mathcal{N})} = 0$ and $R_j^{(0)} = S_j$ for any $t > 0$.

Furthermore, the temporal dimension will also be discretized in segments of Δt. Introduce the additional shorthand notation $N_i^{(l),(m)} = N_i(l\Delta t, m\Delta x)$ and $R_j^{(l),(m)} = R_j(l\Delta t, m\Delta x)$, where $m \in \{0, 1, ..., \mathcal{N}\}$ and $l \in \mathbb{N}$. Then define the following column vectors, describing all the spatial values of the plankton species and resource types at time $l\Delta t$: $\boldsymbol{N_i^{(l)}} = [N_i^{(l),(0)}, N_i^{(l),(1)}, ..., N_i^{(l),(\mathcal{N}-1)}, N_i^{(l),(\mathcal{N})}]^T$ and $\boldsymbol{R_j^{(l)}} = [R_j^{(l),(0)}, R_j^{(l),(1)}, ..., R_j^{(l),(\mathcal{N}-1)}, R_j^{(l),(\mathcal{N})}]^T$. Now it is possible to define the following explicit time integration schemes, using the forward Euler method:

$$\frac{\boldsymbol{N_i^{(l+1)}} - \boldsymbol{N_i^{(l)}}}{\Delta t} = \boldsymbol{\hat{A}^{(l)}} \cdot \boldsymbol{N_i^{(l)}} + \boldsymbol{\hat{B}} \cdot \boldsymbol{N_i^{(l)}} - \boldsymbol{\hat{C}} \cdot \boldsymbol{N_i^{(l)}} \tag{3.24}$$

$$\frac{\boldsymbol{R_j^{(l+1)}} - \boldsymbol{R_j^{(l)}}}{\Delta t} = -\boldsymbol{\hat{D}^{(l)}} + \boldsymbol{\hat{B}} \cdot \boldsymbol{R_j^{(l)}} - \boldsymbol{\hat{C}} \cdot \boldsymbol{R_j^{(l)}} \tag{3.25}$$

Where $\boldsymbol{\hat{A}^{(l)}}, \boldsymbol{\hat{B}}, \boldsymbol{\hat{C}}$ are $\mathcal{N}+1$ by $\mathcal{N}+1$ matrices and $\boldsymbol{\hat{D}^{(l)}}$ is a column vector with size $\mathcal{N}+1$ defined as:

$$\boldsymbol{\hat{A}^{(l)}} = \begin{bmatrix} 0 & 0 & 0 & ... & 0 & 0 \\ 0 & \boldsymbol{\mu_i}(R_1^{(l),(1)}, ..., R_k^{(l),(1)}) - m_i & 0 & ... & 0 & 0 \\ 0 & 0 & \boldsymbol{\mu_i}(R_1^{(l),(2)}, ..., R_k^{(l),(2)}) - m_i & ... & 0 & 0 \\ ... & ... & ... & ... & ... & ... \\ 0 & 0 & 0 & ... & \boldsymbol{\mu_i}(R_1^{(l),(\mathcal{N}-1)}, ..., R_k^{(l),(\mathcal{N}-1)}) - m_i & 0 \\ 0 & 0 & 0 & ... & 0 & 0 \end{bmatrix} \tag{3.26}$$

$$\boldsymbol{\hat{B}} = \frac{\mathcal{D}}{\Delta x^2} \begin{bmatrix} 0 & 0 & 0 & 0 & ... & 0 & 0 & 0 \\ 1 & -2 & 1 & 0 & ... & 0 & 0 & 0 \\ 0 & 1 & -2 & 1 & ... & 0 & 0 & 0 \\ 0 & 0 & 1 & -2 & ... & 0 & 0 & 0 \\ ... & ... & ... & ... & ... & ... & ... & ... \\ 0 & 0 & 0 & 0 & ... & -2 & 1 & 0 \\ 0 & 0 & 0 & 0 & ... & 1 & -2 & 1 \\ 0 & 0 & 0 & 0 & ... & 0 & 0 & 0 \end{bmatrix}; \tag{3.27}$$

$$\boldsymbol{\hat{C}} = \frac{Z(0) \cdot v(0)}{2\Delta x} \begin{bmatrix} 0 & 0 & 0 & ... & 0 & 0 & 0 \\ -Z(\Delta x)^{-1} & 0 & Z(\Delta x)^{-1} & ... & 0 & 0 & 0 \\ 0 & -Z(2\Delta x)^{-1} & 0 & ... & 0 & 0 & 0 \\ 0 & 0 & -Z(3\Delta x)^{-1} & ... & 0 & 0 & 0 \\ ... & ... & ... & ... & ... & ... & ... \\ 0 & 0 & 0 & ... & 0 & Z((\mathcal{N}-2)\Delta x)^{-1} & 0 \\ 0 & 0 & 0 & ... & -Z((\mathcal{N}-1)\Delta x)^{-1} & 0 & Z((\mathcal{N}-1)\Delta x)^{-1} \\ 0 & 0 & 0 & ... & 0 & 0 & 0 \end{bmatrix} \tag{3.28}$$

$$\boldsymbol{\hat{D}^{(l)}} = \begin{bmatrix} 0 \\ \sum_{i=1}^n c_{ji} N_i^{(1),(l)} \boldsymbol{\mu_i}(R_1^{(l),(1)}, R_2^{(l),(1)}, ..., R_k^{(l),(1)}) \\ \sum_{i=1}^n c_{ji} N_i^{(2),(l)} \boldsymbol{\mu_i}(R_1^{(l),(2)}, R_2^{(l),(2)}, ..., R_k^{(l),(2)}) \\ ... \\ \sum_{i=1}^n c_{ji} N_i^{(l),(\mathcal{N}-1)} \boldsymbol{\mu_i}(R_1^{(l),(\mathcal{N}-1)}, R_2^{(l),(\mathcal{N}-1)}, ..., R_k^{(l),(\mathcal{N}-1)}) \\ 0 \end{bmatrix} \tag{3.29}$$

However, it is important to notice that the stability of these schemes are not guaranteed. A specific condition of the form $K\Delta t \leq \Delta x^2$, where K is a real constant, needs to be met. To counteract this, a combination of the implicit backwards Euler scheme and the explicit forward Euler scheme will be considered instead:

$$\frac{\boldsymbol{N_i^{(l+1)}} - \boldsymbol{N_i^{(l)}}}{\Delta t} = \boldsymbol{\hat{A}^{(l)}} \cdot \boldsymbol{N_i^{(l)}} + \boldsymbol{\hat{B}} \cdot \boldsymbol{N_i^{(l+1)}} - \boldsymbol{\hat{C}} \cdot \boldsymbol{N_i^{(l+1)}} \tag{3.30}$$

$$\frac{\boldsymbol{R_j^{(l+1)}} - \boldsymbol{R_j^{(l)}}}{\Delta t} = -\boldsymbol{\hat{D}^{(l)}} + \boldsymbol{\hat{B}} \cdot \boldsymbol{R_j^{(l+1)}} - \boldsymbol{\hat{C}} \cdot \boldsymbol{R_j^{(l+1)}} \tag{3.31}$$

Solving for the $(l+1)$ terms yields the time integration scheme used in the simulations, where I_n denotes an identity matrix with size n:

$$\boldsymbol{N_i^{(l+1)}} = (I_{\mathcal{N}} - \Delta t(\hat{\boldsymbol{B}} - \hat{\boldsymbol{C}}))^{-1} \cdot (I_{\mathcal{N}} + \Delta t \hat{\boldsymbol{A}}^{(l)}) \cdot \boldsymbol{N_i^{(l)}} \tag{3.32}$$

$$\boldsymbol{R_j^{(l+1)}} = (I_{\mathcal{N}} - \Delta t(\hat{\boldsymbol{B}} - \hat{\boldsymbol{C}}))^{-1} \cdot (\boldsymbol{R_j^{(l)}} - \Delta t \hat{\boldsymbol{D}}^{(l)}) \tag{3.33}$$

This time integration scheme has the advantage of incorporating an implicit time integration scheme, which has the property of not enforcing a condition on the size of Δt and Δx to achieve stability. However, an explicit time integration scheme is also incorporated, which means that there still exist a condition for stability in terms of Δt and Δx, but that condition is less strict than the condition if only the forward Euler method (3.24-3.25) was used.

Furthermore to be able to examine the influence of purely advective mass transfer, when no dispersive mass transfer is present, a minor adjustment needs to be made to the model. When no dispersive mass transfer is present, the central difference approximation for the first derivative skips over every node $x = \boldsymbol{i^*} \Delta x$ where $\boldsymbol{i^*}$ is an odd number. This results in the undesirable effect that $N_i^{(l),(i^*)} \to 0$, which is not an accurate depiction of the behaviour of an ecosystem with only advective mass transfer. To counteract this effect an alternative finite difference approximation is used for the first spatial derivative, for $m = 1, 2, ..., \mathcal{N} - 1$:

$$\frac{dN_i^{(m)}}{dx} = \frac{N_i^{(m-1)} - N_i^{(m)}}{\Delta x} \tag{3.34}$$

$$\frac{dR_j^{(m)}}{dx} = \frac{R_j^{(m-1)} - R_j^{(m)}}{\Delta x} \tag{3.35}$$

Which results in a different expression for the matrix $\hat{\boldsymbol{C}}$:

$$\hat{\boldsymbol{C}}' = \frac{Z(0) \cdot v(0)}{\Delta x} \begin{bmatrix} 0 & 0 & 0 & 0 & ... & 0 & 0 & 0 \\ -Z(\Delta x)^{-1} & Z(\Delta x)^{-1} & 0 & 0 & ... & 0 & 0 & 0 \\ 0 & -Z(2\Delta x)^{-1} & Z(2\Delta x)^{-1} & 0 & ... & 0 & 0 & 0 \\ 0 & 0 & -Z(3\Delta x)^{-1} & Z(3\Delta x)^{-1} & ... & 0 & 0 & 0 \\ ... & ... & ... & ... & ... & ... & ... & ... \\ 0 & 0 & 0 & 0 & ... & Z((\mathcal{N}-2)\Delta x)^{-1} & 0 & 0 \\ 0 & 0 & 0 & 0 & ... & -Z((\mathcal{N}-1)\Delta x)^{-1} & Z((\mathcal{N}-1)\Delta x)^{-1} & 0 \\ 0 & 0 & 0 & 0 & ... & 0 & 0 & 0 \end{bmatrix} \tag{3.36}$$

It should be noted that, even if $\mathcal{D} = 0$, this finite difference approximation introduces a small amount of dispersion to the system. This alternative definition for the matrix $\hat{\boldsymbol{C}} = \hat{\boldsymbol{C}}'$ is only used in section (3.4.1), in sections (3.4.2-3.4.5) equation (3.28) is used to define the matrix $\hat{\boldsymbol{C}}$ instead.

Finally, in sections (3.4.4-3.4.5) all the model expansions, that have been covered so far, are combined. In these sections, light intensity is incorporated in the spatial context by changing the definition of $\boldsymbol{\mu_i}(R_1^{(m),(l)}, R_2^{(m),(l)}, ..., R_k^{(m),(l)})$ in the matrices $\hat{\boldsymbol{A}}^{(l)}$, $\hat{\boldsymbol{D}}^{(l)}$ to the one given in equation (3.8):

$$\boldsymbol{\mu_i}(R_1^{(m),(l)}, R_2^{(m),(l)}, ..., R_k^{(m),(l)}, N_1^{(m),(l)}, N_2^{(m),(l)}, ..., N_n^{(m),(l)}) \tag{3.37}$$

$$= min(\frac{r_i R_1^{(m),(l)}}{K_{1i} + R_1^{(m),(l)}}, \frac{r_i R_2^{(m),(l)}}{K_{1i} + R_2^{(m),(l)}}, ..., \frac{r_i R_k^{(m),(l)}}{K_{ki} + R_k^{(m),(l)}}) \cdot \frac{r_i}{Z(m\Delta x) \cdot \omega(m,l)} ln(\frac{L_i + I_{in}}{L_i + I_{in} e^{-Z(m\Delta x) \cdot \omega(m,l)}})$$

Where $\omega(m,l)$ is defined as:

$$\omega(m,l) = H_{bg} + \sum_{i=1}^{n} h_i N_i^{(m),(l)}$$

3.3.1. The dimensionless Péclet number

The added spatial context allows for the introduction of a dimensionless number called the Péclet number. It illustrates a relationship between dispersive and advective mass transfer in a dispersion-advection system. The number can be calculated using the characteristic length $\mathcal{L}$ $[m]$ of the system, the dispersion constant $\mathcal{D}$ $[m^2 s^{-1}]$ and the flow speed v $[ms^{-1}]$:

$$Pe = \frac{v\mathcal{L}}{\mathcal{D}} = \frac{[m \cdot s^{-1}] \cdot [m]}{[m^2 \cdot s^{-1}]} \tag{3.38}$$

This definition implies that a low Péclet number indicates that the system's mass transfer is dominated by dispersive mass transfer, and a high Péclet number indicates that the system's mass transfer is dominated by advective mass transfer.

3.4. Behaviour predicted by the model with the spatial context

Now that the spatial context has been properly introduced and added to the model several relevant questions emerge. Firstly, what is the influence of advective and dispersive mass transfer, with and without light intensity, on the spatial and temporal distribution of the species abundances? Secondly, does behaviour predicted by the original model (2.2-2.3), the paradox of plankton and the emergence of limit cycles, reoccur in the model constructed in the previous section (3.3) and under which conditions?

To gain insight into these questions several systems will be simulated. Firstly, a system with one resource type and one plankton species is observed where only advective transfer is present. Secondly, a system with three resource types and three plankton species is observed where both dispersive and advective mass transfer is present and limit cycles occur, which is behaviour that is predicted by the original model (2.2-2.3). Thirdly, a system with three resource types and four plankton species is observed where the paradox of plankton appears. For this system the influence of changing the supply concentrations S_j, and the effect of having either dispersive mass transfer or advective mass transfer, or both, is observed. Additionally, several simulations are done for this system, while maintaining the same ratios between the mortality m_i and growth r_i rates, to show that the paradox of plankton may appear while a wide range of limit cycles with different frequencies are present. Fourthly, a system with three resource types and three plankton species, where both the spatial context and light intensity are incorporated, is simulated with a region with increased background turbidity to show its influence on the spatial distribution of the species abundances of the plankton species, and the potential emergence of a dominant plankton species if one species is better at consuming light intensity than the other plankton species. Finally, for this system, a region is added that is significantly more shallow than the average depth of the river to show how the plankton species drift faster in that region.

3.4.1. 1 resource type and 1 plankton species

The first system examined has one resource type and one plankton species and only advective mass transfer. This simulation is done to observe the effect of advective mass transfer on the spatial distribution of the species abundance N_1. The parameters of the system are:

$\mathcal{L}$	6
Z	1.00
$\mathcal{D}$	0
S_1	1.00
m_1	0.25
r_1	1.00

$$K = \begin{bmatrix}1.00\end{bmatrix}$$

$$c = \begin{bmatrix}0.10\end{bmatrix}$$

$$\begin{bmatrix}R_1(0,x)\end{bmatrix} = \begin{bmatrix}1.00\end{bmatrix}$$

$$\begin{bmatrix}N_1(0,x)\end{bmatrix} = \begin{bmatrix}0.11\end{bmatrix}$$

The boundary conditions defined in equations (3.15-3.18) are used. Additionally, the flow speed of the river v will be systematically varied to observe the influence of only advective mass transfer, which is shown in figure 3.7.

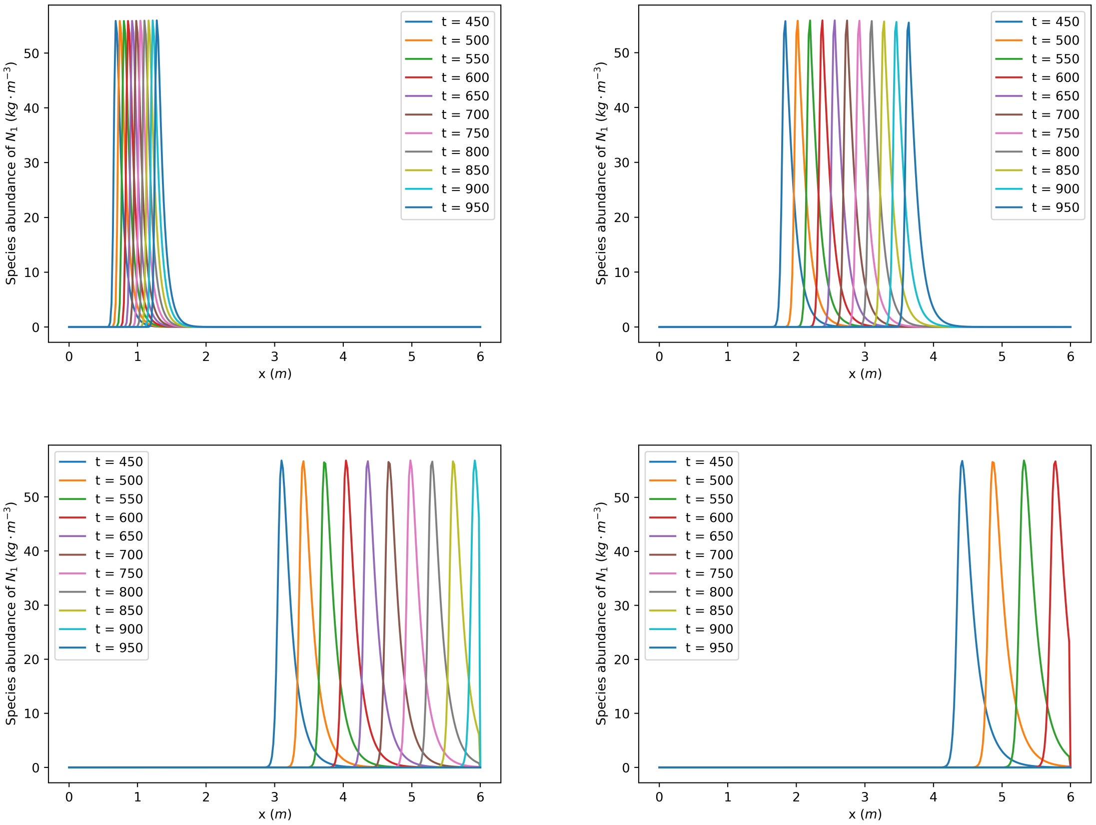

Figure 3.7: The spatial distribution of the species abundance of N_1, recorded at $t = 3950$. The top left and right graph have flow speeds v respectively set to 0.02 and 0.03. The bottom left and right graphs have flow speeds v respectively equal to 0.04 and 0.05.

A peak moving to the right appears in every system. The speed at which this peak travels depends on the flow speed v. The width of this peak is also influenced by the flow speed, becoming wider for a larger flow speed v. Furthermore, the amplitude of every peak is not influenced by the flow speed and does not decrease over time. This implies that regardless of the length of the river $\mathcal{L}$, the peak will travel over the entire length of the river. The peak disappears once it reaches the right end of the river due to the boundary condition $N_1(t, \mathcal{L}) = 0$. Initially, the plankton further down the river are able to survive for a short amount of time due to the initial resources present there, but they quickly go extinct when they have consumed all the resources available. Only the plankton around the beginning of the river are able to survive long enough to be able to consume the newly supplied resources at $x = 0$. To summarize, the peak appears due to the initial amount of plankton present at $t = 0$ close to the beginning of the river. (A consequence of this is that no new peak will appear once the peak has disappeared at the right side of the river.) This behaviour can be observed in figure 3.8, which are visualizations of the species abundance N_1 over time and position.

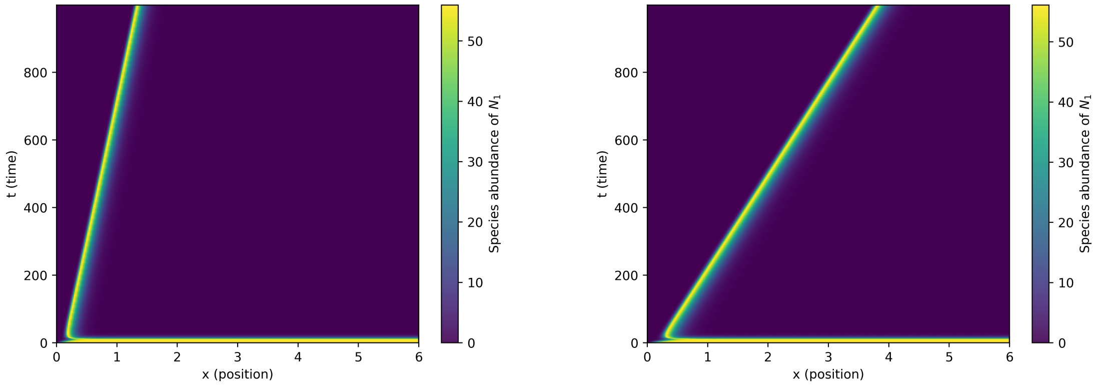

Figure 3.8: The spatial distribution of the species abundance N_1 against time t and position x. The left and right graph have flow speeds v respectively set to 0.02 and 0.03.

If the boundary condition at the left side of the river is changed to $N_1(t, 0) = \beta > 0$ such that there is a small supply of new plankton into the system, a new peak appears with a higher amplitude. However, this peak's position and amplitude is invariant with respect to time, as shown in figure 3.9.

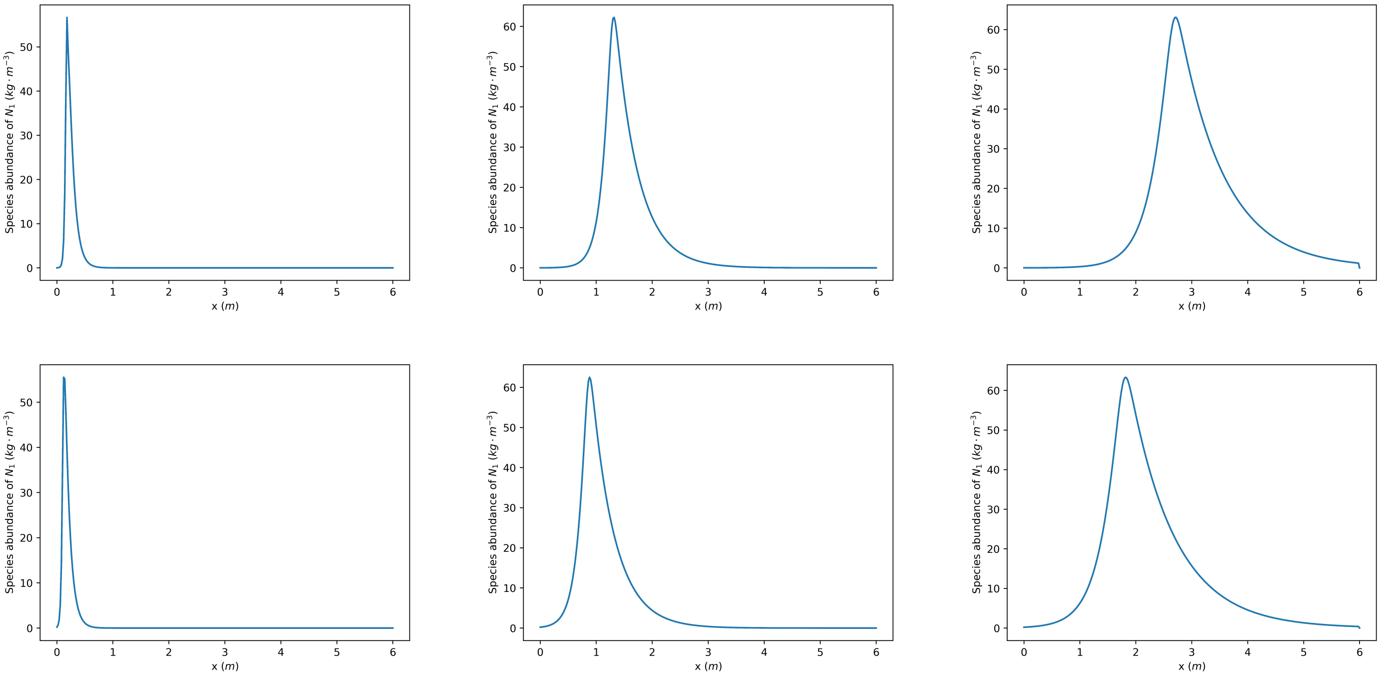

Figure 3.9: The spatial distribution of the abundance of the plankton species for a system with a constant supply of plankton into the system. For the top graphs $\beta = 0.01$ and for the bottom graphs $\beta = 0.21$. The left, middle, and right graphs have flow speeds v respectively equal to 0.02, 0.1 and 0.2. The initial distribution of plankton $N_1(x, 0) = 0.11$ converges to these asymmetrical peaks over time.

It can be seen how the width and the x location of the peaks increases as the flow speed v increases. Furthermore, the x location of the peak also depends on the constant supply at the left side of the river β. A smaller supply causes the peak to appear further along the river, and vice versa. This implies that it is possible to control the location of the center of the peak by varying this supply β. Furthermore, by observing the species abundance of N_1 against time and position, see figure 3.10, it is found any new plankton supplied at $x = 0$ follows an identical curve against time, regardless of the time at which this plankton was introduced to the system. This is due there only being advective mass transfer present in this system, which implies that a plankton further down the river is not influenced by new plankton that are introduced at the beginning of the river. This explains the appearance of an asymmetrical peak that is invariant with respect to time.

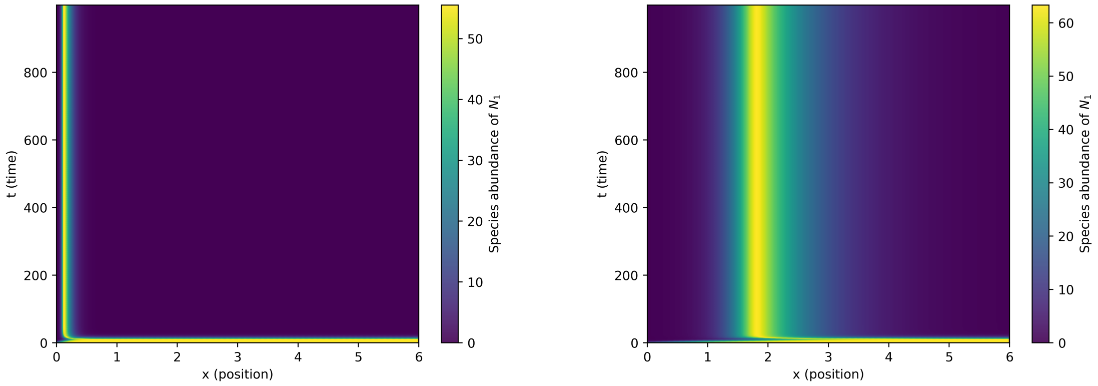

Figure 3.10: The spatial distribution of the species abundance N_1 against time t and position x. The left and right graph have flow speeds v respectively set to 0.02 and 0.2. For both graphs a constant amount of plankton is supplied at the beginning of the river $\beta = 0.21$.

3.4.2. 3 resource types and 3 plankton species

The second system examined has three resource types and three plankton species. This system is chosen because it is known to be the simplest system, without the spatial context, where only unstable equilibrium solutions are present. This section aims to show that behaviour predicted by the original chemostat model (2.2-2.3), the appearance of limit cycles, reoccurs in the model constructed in section (3.3). Furthermore, it aims to show the effect of advective mass transfer versus dispersive mass transfer on the spatial distribution of the species abundances N_i. For this system, the same parameters as in section (2.4) are used. The initial values are defined as $N_1(0,x) = 0.11$, $N_2(0,x) = 0.12$, $N_3 = 0.13$, $R_1(0,x) = S_1$, $R_2(0,x) = S_2$ and $R_3(0,x) = S_3$. The segment of the river considered has a length of $\mathcal{L} = 40$ and constant depth $Z = 1.00$. The dispersion constant is defined as $\mathcal{D} = 2.5$ and the flow speed is defined as $v = 1.25$. This results in a Péclet number of $Pe = 20$. The simulation yields a limit cycle where all the three species coexist, see figure 3.11.

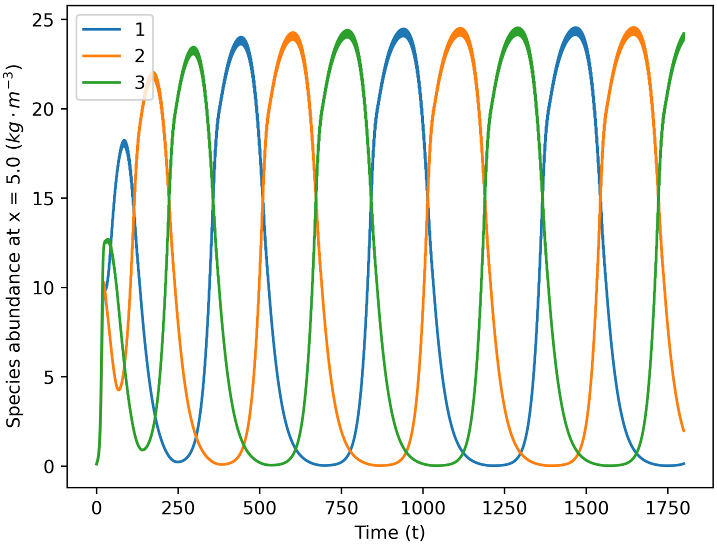

Figure 3.11: The graph visualizes the species abundance at $x = 5.0$ for every respective plankton species. Note that the simulation stabilizes to a limit cycle after $t = 400$.

This indicates that introducing the spatial context still allows for limit cycles to appear. However, it must be noted that the cycle has the same characteristics as a heteroclinic cycle. Plankton species repeatedly approach near zero values, close to 0.01, before reemerging and growing to a value close to 25.0.

Graphing the species abundance for plankton species N_1 along the spatial axis shows how the spatial distribution shares characteristics with an asymmetrical peak, as shown in figure 3.12. Similar distributions, with the same characteristics, are found for the species abundance of plankton species N_1 and N_2.

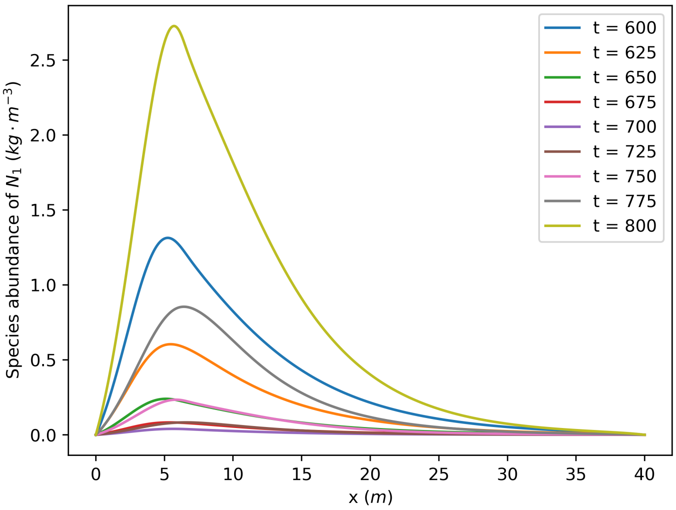

Figure 3.12: The spatial distribution of the species abundance of plankton species N_1, recorded at several timestamps. Along the spatial axis it can be seen how the distribution of the species abundance shares characteristics with an asymmetrical peak. The spatial distribution of species abundance stays relatively constant over time. However, the amplitude of the distribution does vary over time. Specifically for this system with a limit cycle, over time the amplitude of the distribution oscillates between a near-zero value and 25.00.

Increasing the flow speed v, while keeping the dispersion constant $\mathcal{D}$ and $\mathcal{L}$ fixed at the same values, increases the x position of the center of the peak, see figure 3.13.

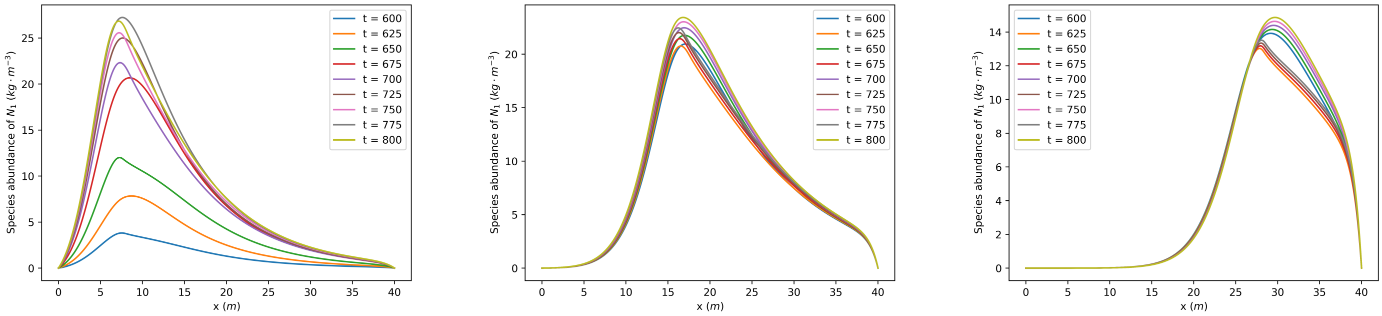

Figure 3.13: The spatial distribution of the species abundance N_1, recorded at several timestamps. The left, middle and right graph have a flow speed v respectively set to 1.75, 2.35 and 2.50.

Further varying the flow speed v, gives insight into conditions for which cycles and stable equilibrium solutions appear, see figure 3.14.

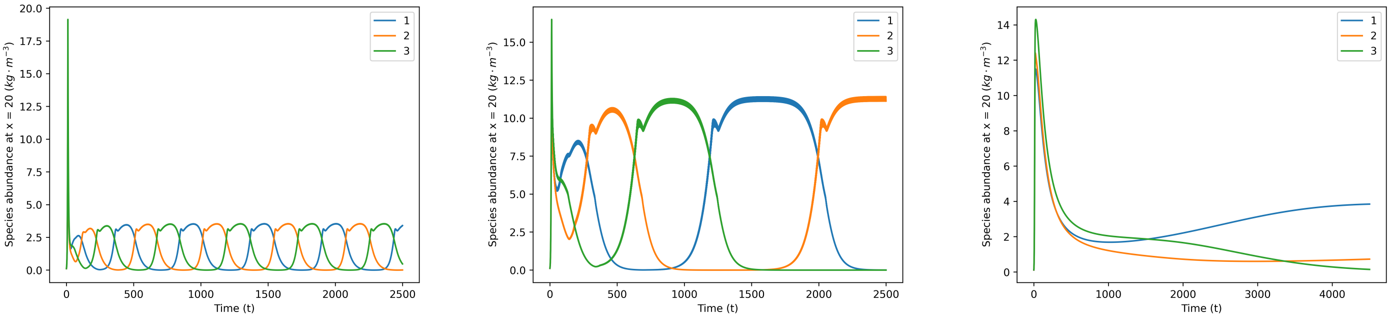

Figure 3.14: The graph visualizes the species abundance at $x = 20.0$ for every respective plankton species. Several values for flow speed v are used, while keeping the dispersion constant $\mathcal{D} = 2.5$ and the length of the river $\mathcal{L} = 40$ fixed. The left, middle and right graphs have Péclet numbers respectively equal to 20, 32 and 40. Note how the cyclic behaviour is not present in the right graph.

In figure 3.14 it is observed how the amplitude and period of the cycle increases as the Péclet number increases. The limit cycle at $x = 20$ shares characteristics with a heteroclinic cycle, where a majority of the time one of the three plankton species is extinct. (However, as mentioned in section (2.4.2) it is expected that these heteroclinic cycles can be converted to limit cycles by varying specific parameters in the system.)

Increasing the Péclet number further to 40.0 results in the disappearance of the cyclic behaviour. The system will then approach a stable equilibrium where one of the three plankton species is extinct.

3.4.3. 3 resource types and 4 plankton species

The third system examined has three resource types and four plankton species. This system is chosen because it is the simplest system in the original chemostat model (2.2-2.3) where the paradox of plankton is present. However, in the more realistic model constructed in section (3.3), with dispersive and advective mass transfer, it is unknown if the paradox of plankton still appears.

The first aim of this section is to show that the paradox of plankton can still appear, by letting four plankton species coexist on three resource types, while only dispersive mass transfer is present. The second aim of this section is to show the dependency of the coexistence, of the four plankton species while no advective mass transfer is present, on the concentration of every resource type supplied at the beginning of the river S_j. The third aim of this section is to show the influence of dispersive mass transfer, without any advective mass transfer, on the spatial distribution of the species abundances N_i. The fourth aim of this section is to show that the paradox of plankton can occur when both dispersive and advective mass transfer is present, and that the resulting coexistence depends on the dispersive mass transfer being more dominant than the advective mass transfer. The fifth aim of this section is to show that the limit cycles that occur, when four plankton species coexist on three resource types, can have several frequencies as long as the ratios between the mortality m_i and growth rates r_i are conserved.

The system's parameters that help achieve the first aim are:

$\mathcal{L}$	40
Z	1.00
$\mathcal{D}$	0.25
v	0
S_1	$10-\alpha$
S_2	10
S_3	$10+\alpha$
m_1	0.25
m_2	0.25
m_3	0.25
m_4	0.25
r_1	1.00
r_2	1.00
r_3	1.00
r_4	1.00

$$K = \begin{bmatrix} 1.00 & 0.90 & 0.30 & 1.04 \\ 0.30 & 1.00 & 0.90 & 0.71 \\ 0.83 & 0.30 & 1.00 & 0.46 \end{bmatrix}$$

$$c = \begin{bmatrix} 0.04 & 0.07 & 0.04 & 0.10 \\ 0.08 & 0.08 & 0.10 & 0.10 \\ 0.14 & 0.10 & 0.10 & 0.16 \end{bmatrix}$$

$$\begin{bmatrix} R_1(0,x) & R_2(0,x) & R_3(0,x) \end{bmatrix} = \begin{bmatrix} 10-\alpha & 10 & 10+\alpha \end{bmatrix}$$

$$\begin{bmatrix} N_1(0,x) & N_2(0,x) & N_3(0,x) & N_4(0,x) \end{bmatrix} = \begin{bmatrix} 0.11 & 0.12 & 0.13 & 0.10 \end{bmatrix}$$

The first example shows that, by setting $\alpha = 2.5$, it is still possible for four plankton species to coexist on three resources while only dispersive mass transfer is present, see figure 3.15.

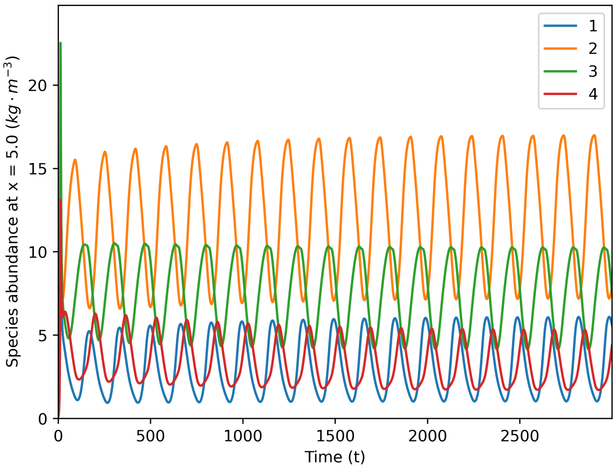

Figure 3.15: The graph visualizes the species abundance at $x = 5.0$ for every respective plankton species. Note that the simulation stabilizes to a limit cycle after $t = 2000$.

This shows that the paradox of plankton can still appear even when introducing the spatial context of a flowing river and only dispersive mass transfer is present.

Furthermore, to achieve the second aim, it is shown that the coexistence of the plankton species significantly depends on the concentration of the supplied resources S_1, S_2 and S_3 at $x = 0$. By systematically decreasing the value of α the cyclic behaviour disappears and a stable equilibrium solution appears. This can be observed in figure 3.16.

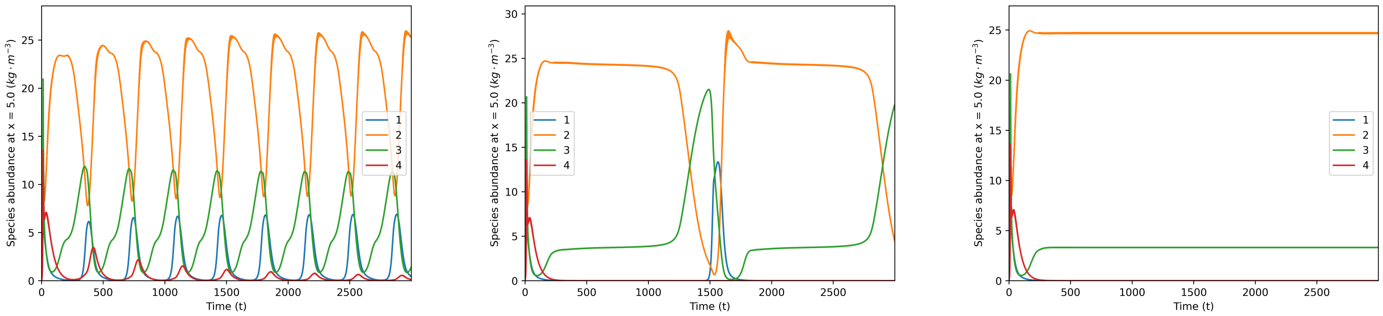

Figure 3.16: The graph visualizes the species abundance at $x = 5.0$ for every respective plankton species. For the left, middle and right graph α is respectively set to 1.975, 1.8895 and 1.875. The coexistence of the four plankton species disappears as the limit cycle vanishes. Eventually, two plankton species go extinct as the system approaches a stable equilibrium.

Furthermore, in figure 3.17, it is shown how a different stable equilibrium, emerges if α is systematically increased instead. The oscillatory behaviour, when the four plankton species coexist, eventually disappears as time progresses and the plankton species converge to an asymptotically stable equilibrium solution where plankton species N_1 has gone extinct.

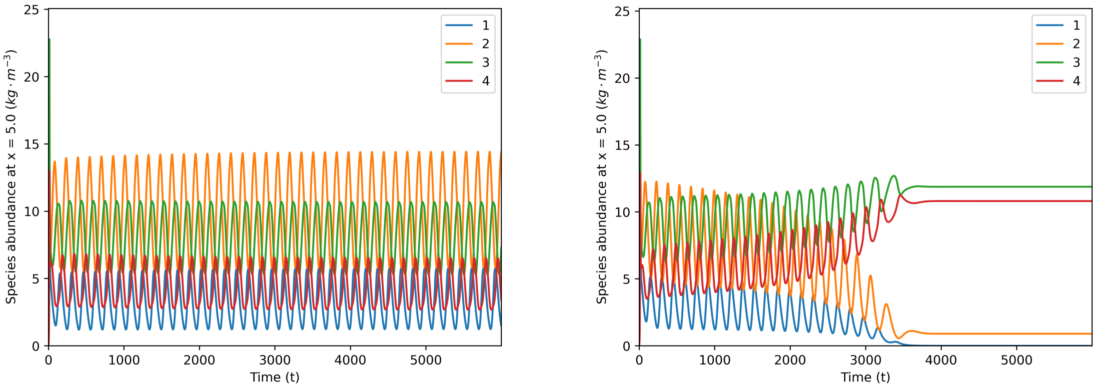

Figure 3.17: The graph visualizes the species abundance at $x = 5.0$ for every respective plankton species. For the left and right graph α is respectively set to 2.6 and 2.65. Once again the coexistence of the four plankton species disappears as the limit cycle vanishes. Eventually, one plankton species goes extinct as the system approaches a stable equilibrium. Note that this is a different equilibrium solution than shown in figure (3.16).

This implies that the paradox of plankton only emerges for a specific range of S_1, S_2, S_3. For this example, given that $S_2 = 10$, that range is $7.4 \leq S_1 \leq 8.0$ and $12.0 \leq S_3 \leq 12.6$. If these variables are outside of this range, the model converges to a stable equilibrium solution where one or more plankton species are extinct.

To achieve the third aim, the influence of pure dispersive mass transfer is observed in figure 3.18. The flow speed v is kept at 0 and $\alpha = 2.15$. The dispersion constant $\mathcal{D}$ will be systematically varied to observe how an asymmetric peak appears with an oscillating amplitude.

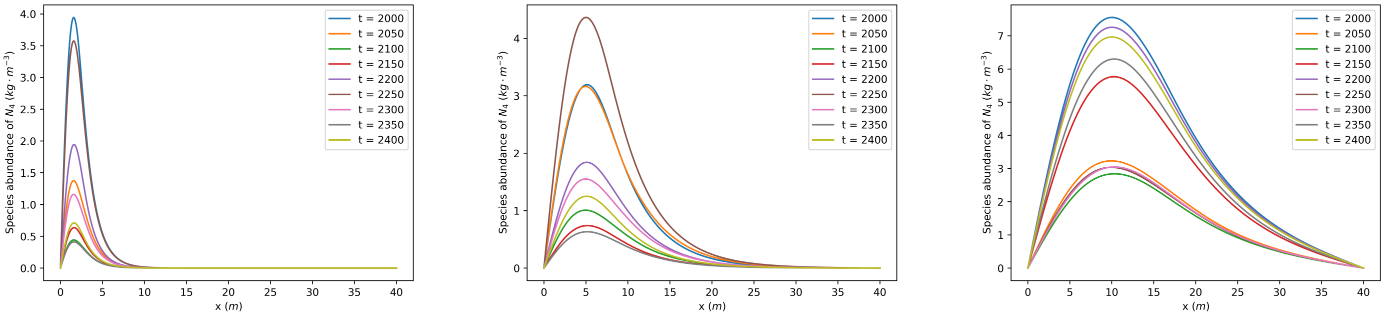

Figure 3.18: The spatial distribution of the species abundance N_4, recorded at several timestamps. The left, middle and right graph have a dispersion constant $\mathcal{D}$ respectively set to 0.5, 5.0 and 20.0.

Furthermore, the width of the peak increases as the dispersion constant $\mathcal{D}$ increases. This can be validated intuitively by realizing that a higher dispersion constant $\mathcal{D}$ implies that the resources entering the river spread out further before the plankton species can consume them. This in turn implies that plankton species even further down the river can still grow to significant sizes due to resources being present there.

Along the temporal axis, similar behaviour as in figure 3.15 is observed for all values of $\mathcal{D} \leq 20.0$. The only difference is that the amplitudes of these limit cycles, at the same $x = 5.0$ coordinate, vary for different values of $\mathcal{D}$ due to the center of the asymmetrical peak shifting to a new location.

This cyclic behaviour disappears when the dispersive constant $\mathcal{D}$ becomes significantly larger with respect to the length of the river. Then a stable equilibrium solution is introduced and one of the four plankton species goes extinct, as shown in figure 3.19. Furthermore, due to no cyclic behaviour being present it is observed how the amplitude of the asymmetrical peak does not vary over time anymore.

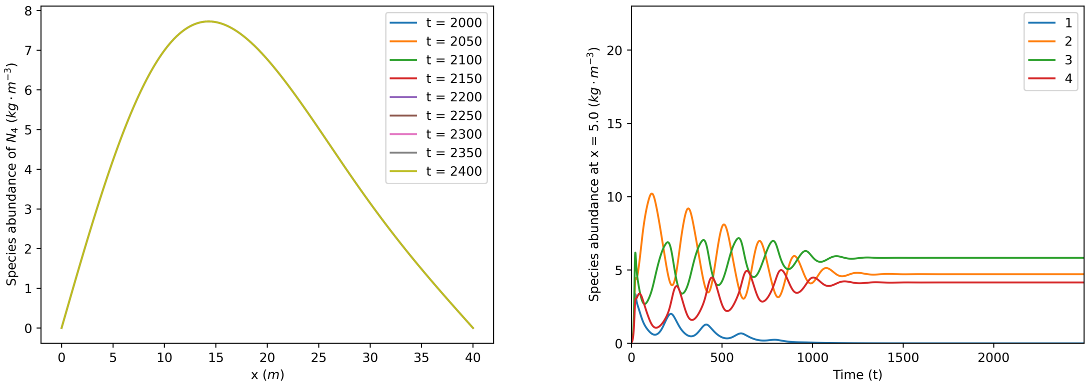

Figure 3.19: The left graph visualizes the spatial distribution of the species abundance N_4, recorded at several timestamps. The right graph visualizes the species abundance at x = 5.0 for respective plankton species

Note how the amplitude of the asymmetrical peak, describing the spatial distribution of N_4, stays invariant with respect to time. Additionally, the spatial distributions of the species abundances N_2 and N_3, not shown, also approach an asymmetrical peak that does not change over time.

Now, to achieve the fourth aim, the influence of advective mass transfer is analyzed. By setting $\alpha = 2.5$ the system is reverted to a state where it is known that the coexistence of four plankton species is possible. Motivated by the simulations shown in figure 3.14, it is presumed that the paradox of plankton occurs when dispersive mass transfer is more dominant than advective mass transfer. Therefore, in figure 3.20, it can be seen that by keeping the dispersion constant $\mathcal{D} = 2.5$ and the length of the river

$\mathcal{L} = 40$ fixed and systematically altering the flow speed v it is found that the coexistence of four plankton species is possible when the Péclet number is lower than 4.0. For example, when the Péclet number is equal to 0.4 a simulation occurs similar to figure 3.15. It shows that it is likely, for this system, that this system converges to a stable equilibrium solution, where the biodiversity is limited by the different types of resources supplied to the system, when the Péclet number is larger than 4.0.

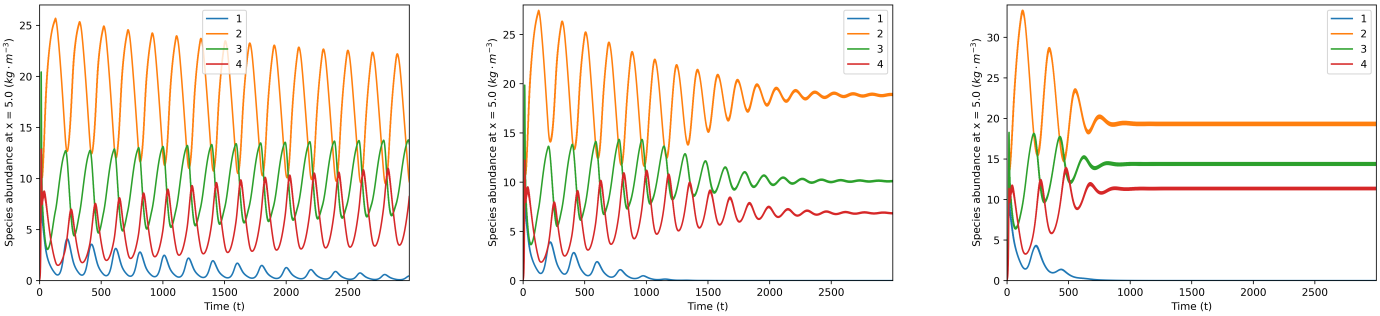

Figure 3.20: The graphs visualizes the species abundance at $x = 5.0$ for every respective plankton species. The left, middle and right graph have Péclet numbers respectively equal to 4.0, 5.6 and 12.0.

To achieve the fifth aim, it is observed that the system has the property that $r_i = r = 1.00\ [t^{-1}]$ and $m_i = m = 0.25\ [t^{-1}]$ for all $\forall i \in \{1, 2, 3, 4\}$. If simulations are done for modified systems where both these growth and mortality rates are multiplied by the same constant $\gamma \in \mathbb{R}$: $r = 1.00 \cdot \gamma$ and $m = 0.25 \cdot \gamma$, a dimensionless number can be constructed that remains constant regardless of the value of γ:

$$\frac{r}{m} = \frac{1.00 \cdot \gamma}{0.25 \cdot \gamma} = \frac{[t^{-1}]}{[t^{-1}]} \tag{3.39}$$

The species abundance for every plankton species at several timestamps, when doing simulations for several values of γ, where $\mathcal{D} = 2.5;\ v = 0.3;\ \alpha = 2.0$, is shown in figure 3.21.

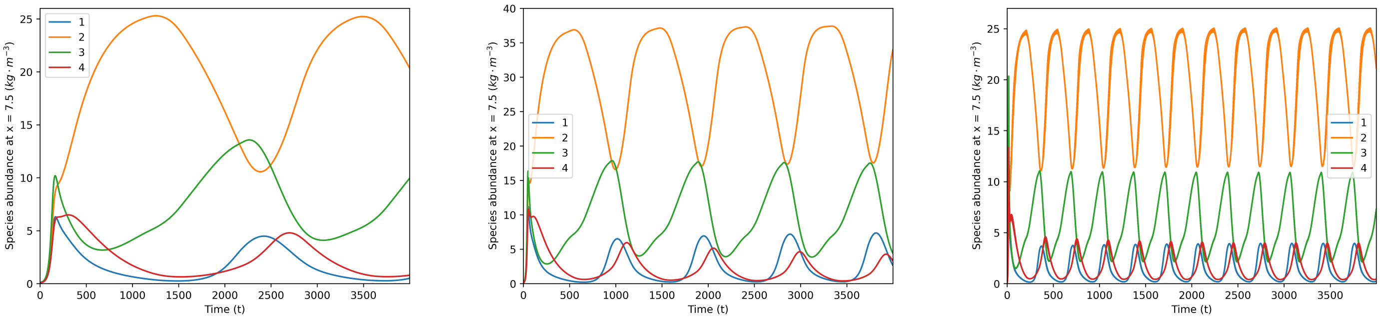

Figure 3.21: The graphs visualizes the species abundance at $x = 7.5$ for every respective plankton species. The left, middle and right graph have γ respectively set to 0.10, 0.25 and 0.75.

Observe how (the ratios of) the cycle's amplitudes are not significantly altered. Furthermore, the limit cycle's period increases as γ becomes smaller. However, there are limits to this relation. When $\gamma = 0.05$ the coexistence of the four plankton species disappears as an asymptotically stable equilibrium solution is introduced. When $\gamma = 1.5$ limit cycles still appear, however plankton species N_1 goes extinct, as shown in figure 3.22.

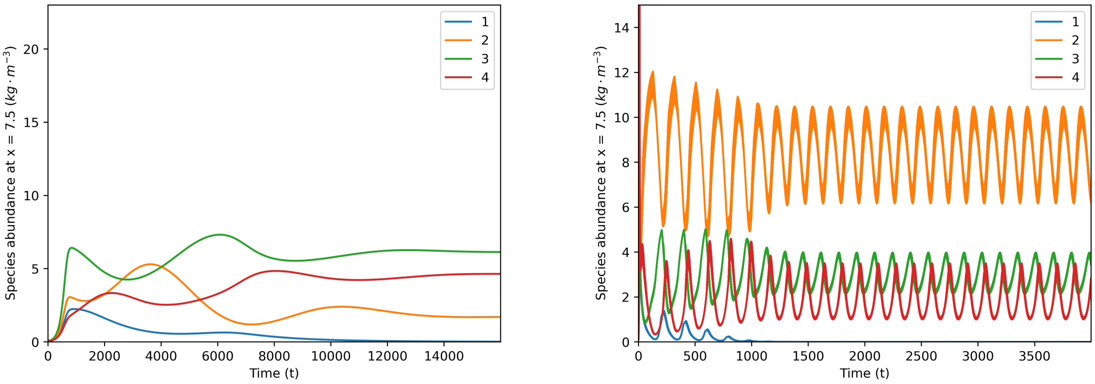

Figure 3.22: The graphs visualizes the species abundance at $x = 7.5$ for every respective plankton species. The left and right graph have γ respectively set to 0.05 and 1.5.

It is concluded that if the paradox of plankton appears for a system, where all the plankton species have identical growth and mortality rates, it is possible to maintain the paradox even if these rates change. The requirement is that the ratio between the growth and mortality rate $\frac{r}{m}$ remains constant and that the absolute difference $M_1 < r - m < M_2$ for certain values $M_1, M_2 \in \mathbb{R}$.

3.4.4. Effect of background turbidity and light consumption

This section will observe the effect of adding a region in the river with an increased amount of background turbidity. This is done by incorporating both the spatial context and light intensity as described in equation (3.37). The first aim of this section is to show the effect of adding an area with increased background turbidity to the spatial distribution of the species abundances of the plankton species. The second aim of this section is to show how a plankton species can become dominant if it is better at consuming light intensity than the other plankton species in the system. The system examined has three resource types and three plankton species. The same parameters are used as in section (2.4.2) with the addition of:

$\mathcal{L}$	25
Z	1.00
$\mathcal{D}$	2.5
v	0.25
I_{in}	2.5

$$\begin{bmatrix} L_1 & L_2 & L_3 \end{bmatrix} = \begin{bmatrix} 2.00 & 2.00 & 2.00 \end{bmatrix}$$

$$\begin{bmatrix} h_1 & h_2 & h_3 \end{bmatrix} = \begin{bmatrix} 0.01 & 0.01 & 0.01 \end{bmatrix}$$

$$H_{bg}(x) = \begin{cases} \theta\,; & 8 < x < 12 \\ 0.01\,; & else \end{cases}$$

$$\begin{bmatrix} R_1(0,x) & R_2(0,x) & R_3(0,x) \end{bmatrix} = \begin{bmatrix} 10 & 10 & 10 \end{bmatrix}$$

$$\begin{bmatrix} N_1(0,x) & N_2(0,x) & N_3(0,x) \end{bmatrix} = \begin{bmatrix} 0.11 & 0.12 & 0.13 \end{bmatrix}$$

Notice how in the region $8 < x < 12$ the background turbidity will be altered by the constant $\theta \in \mathbb{R}$, this implies that in this river the water is less clear. Outside of this region the river will be assumed to have clearer water, which implies a lower background turbidity. This is done to help achieve the first aim of this section. Furthermore, the system has a constant depth of $Z = 1.00$. The spatial distributions for the species abundances of the plankton species for this system are shown in figure 3.23.

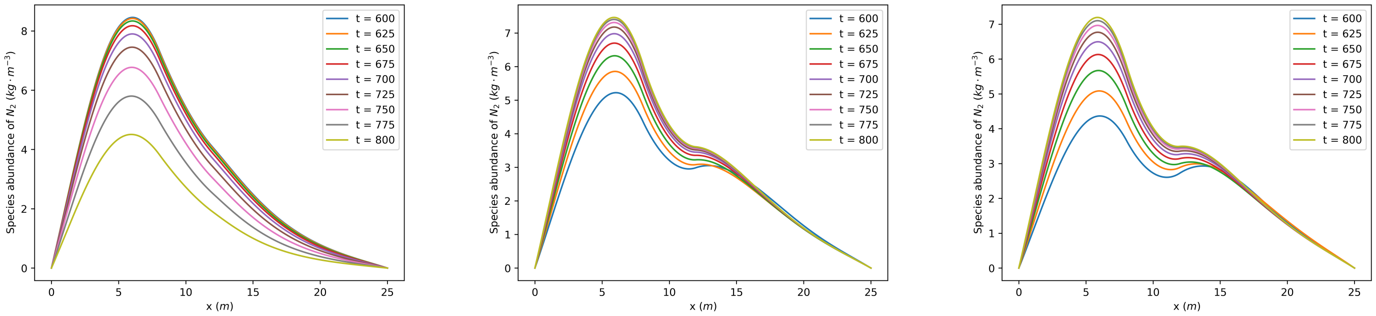

Figure 3.23: The spatial distribution of the species abundance N_1. The left, middle and right graph have θ values respectively set to 3.00, 15.0 and 30.0. Note how there is a sudden decrease in the peak's amplitude in the region $8 < x < 12$. The other species abundances N_2, N_3 have similar spatial distributions that also contain this sudden decrease in amplitude for $8 < x < 12$.

It is observed how with little background turbidity an asymmetrical peak forms, and when a large amount of background turbidity is added to the system in the region $8 < x < 12$, the peak's amplitude will decrease in this region.

Additionally, for the second aim of this section, the effect of altering the half-saturation constant for light L_i is observed. In general, for a plankton species N_i, if L_i becomes lower then the species becomes more dominant. This is shown in figure 3.24.

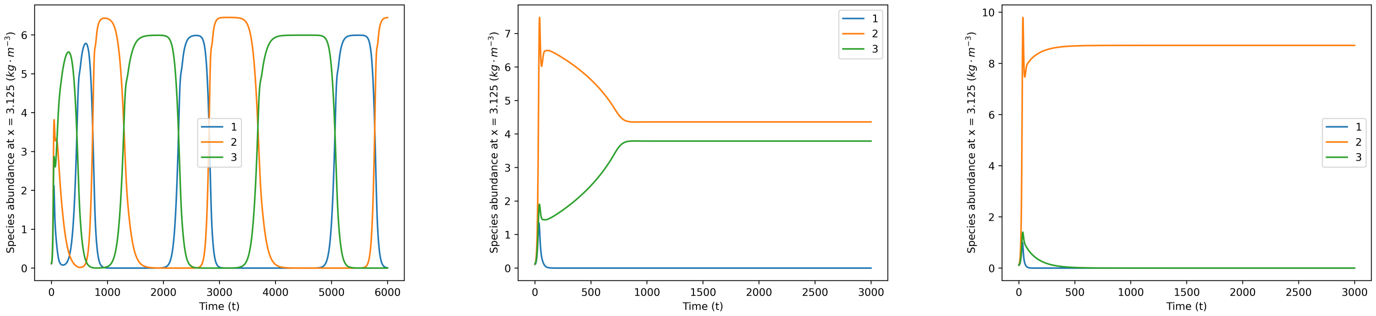

Figure 3.24: The graphs visualize the species abundance at $x = 3.125$ for every respective plankton species over time. The left, middle and right graph have L_2 values respectively set to 1.90, 1.60 and 1.40. For all the graphs $\theta = 3$ and $L_1 = L_3 = 2.00$.

Note how in the left graph the plankton species N_2 grows slightly better under the influence of light than the other plankton species N_1 and N_3 due to $L_2 < L_1$ and $L_2 < L_3$. However, this advantage does not introduce any stable equilibrium solutions. However, when $L_2 = 1.60$, species N_2 becomes dominant, a stable equilibrium solution is introduced where $N_2 > 0$, $N_3 > 0$ and $N_2 = 0$. This removes the cyclic behaviour of the three plankton species. When L_2 is reduced even further to $L_2 = 1.40$ the plankton species N_2 becomes so dominant that the only stable equilibrium solution of this system is one where $N_2 > 0$ and $N_1 = N_3 = 0$.

3.4.5. Effect of varying depth

This section aims to show the effect of adding a region in the river that is significantly more shallow than the average depth of the river on the spatial distribution of the species abundances of the plankton species. Due to the condition that the volumetric flux is constant, it is expected that the river flows significantly faster in this specific region in the river.

The same parameters as in the previous section (3.4.4) are used, with $\theta = 0.01$, however the river's depth is now defined as:

$$Z(x) = \begin{cases} \phi\,; & 8 < x < 12 \\ 10\,; & else \end{cases} \tag{3.40}$$

The constant $\phi \in \mathbb{R}$ defines how shallow the river is in the region $8 < x < 12$. When choosing values for ϕ, one needs to realize that, due to the model expansions, the system has grown in size substantially. Not accounting for initial conditions, the current system with three plankton species and three resource types is described by 35 unique variables. As a consequence, it gets more challenging to determine the influence of any individual variable. To still obtain insight into the influence of adding a shallower region, a non-realistic extreme value of $\phi = 0.01$ will first be simulated. The spatial distributions of the species abundances of all the plankton species are shown in figure 3.25.

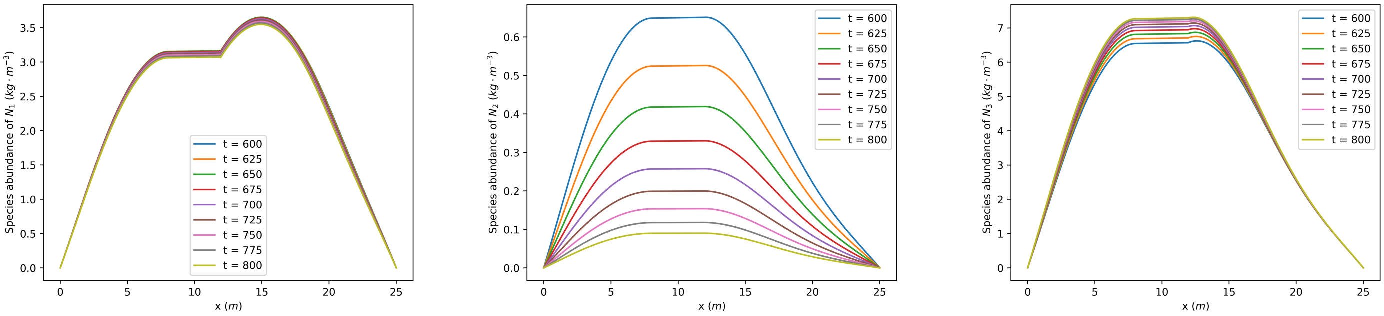

Figure 3.25: The spatial distribution of the species abundances N_1, N_2 and N_3 for $\phi = 0.01$. Note how every spatial distribution becomes almost horizontal in the region $8 < x < 12$.

Intuitively, figure 3.25 can be understood by imagining that the river flows incredibly fast in the region $8 < x < 12$. In this region, the plankton are quickly transported from $x = 8$ to $x = 12$ with little time to consume any resources. This is the reason why an almost flat line appears in the region $8 < x < 12$. To observe a more realistic situation, the simulation is repeated with a value $\phi = 0.75$, see figure 3.26.

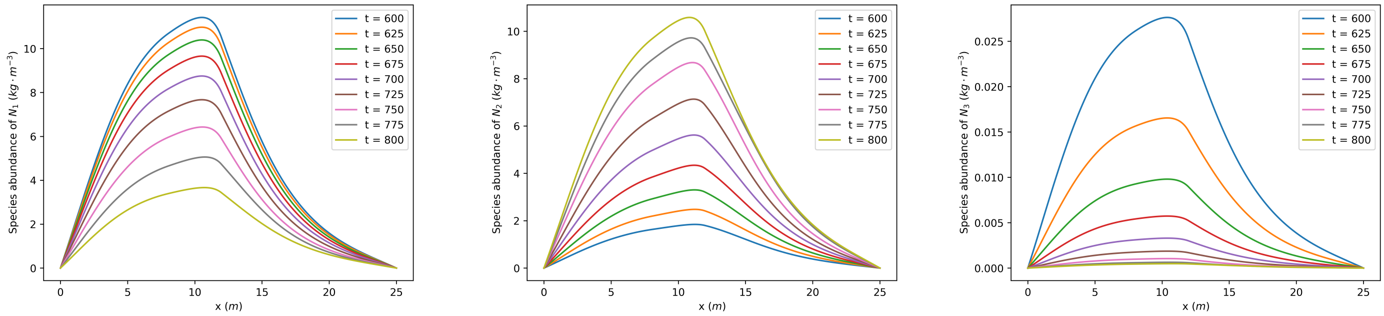

Figure 3.26: The spatial distribution of the species abundances N_1, N_2 and N_3 for $\phi = 0.75$. Note how every spatial distribution increases linearly over time in the region $8 < x < 12$.

Now it can be observed in figure 3.26 that the plankton has more time to consume resources in the region $8 < x < 12$. This is the reason why, when $\phi = 0.75$, the plankton species slowly increase in the region $8 < x < 12$ instead of remaining almost constant, which was the case with $\phi = 0.01$. If ϕ is increased even more the spatial distribution will start to approach the shape of a smooth asymmetrical peak.

4

Conclusion and discussion

The goal of this report was to determine when the principle of competitive exclusion holds and to see whether and when the paradox of plankton exist if more realistic elements, light intensity and dispersive and advective mass transfer, are incorporated in the original model (2.1). New insight was obtained regarding this goal. When an ecosystem exists where there are more plankton species present than the principle of competitive exclusion allows, introducing a dominant plankton species removes the previously achieved biodiversity. A dominant plankton species is defined as a species that allows an asymptotically stable equilibrium solution, with a region of convergence equal to the domain of the system, to exist in the ecosystem. The presence of a dominant plankton species guarantees that the principle of competitive exclusion holds, the number of different types of resources acting as an upper bound on the amount of species that can coexist in the system.

It was found that a necessary condition for the paradox of plankton is that all the equilibrium solutions in the system are unstable, if it is assumed that any asymptotically stable equilibrium solution has a region of convergence equal to the domain of the system. If this condition is not met the principle of competitive exclusion will be satisfied.

Additionally, this report provides a systematic approach to determine whether a plankton species can be introduced to a pre-existing system without removing previously achieved biodiversity that disregarded the principle of competitive exclusion. This is done by first calculating all the possible equilibrium solutions, where the new plankton species is present in the system, with the algorithm described in section (2.2.5), and then using the linear stability analysis described in section (2.3.1) to check whether any stable equilibrium solutions are introduced when adding the new plankton species. Example code that uses this approach is provided in the appendix.

Furthermore, it was proven that in a simplified system, where all the plankton species have a mortality rate equal to the turnover rate of the chemostat model (2.2-2.3), a minimum of three resource types need to be present to allow only unstable equilibrium solutions to exist, which was hypothesized by Huisman & Weissing (1999). Furthermore, it was found that the stability of the equilibrium solutions strongly depends on the amount of every resource present in the plankton species: c_{ji}.

It was motivated that these insights also hold in a more realistic context under certain conditions. When the spatial context of a flowing river, with dispersive and advective mass transfer, is added to the original model it was still possible for the paradox of plankton to appear. When the original model predicted that the paradox of plankton appeared for a system with three resource types and four plankton species (2.4.3), it was observed that recreating that system in the more realistic model (3.4.3), by reusing all parameters from the original model except for the supply concentrations of the resources S_j, also caused the paradox of plankton to appear under certain conditions, see figure 3.17. The first condition is that the diffusive mass transfer needs to be dominant over the advective mass transfer in the river, see figure 3.20. The second condition is that the diffusive mass transfer cannot be too large with respect to the length of the river, see figure 3.19. Thus it was observed for this system that, when these conditions were met, the appearance of the paradox of plankton, and the temporal distribution of the species abundances of the plankton species, was primarily determined by the original model. As a result, the paradox of plankton could be maintained for broad ranges of dispersive and advective mass transfer rates. In contrast, it was observed that the spatial distributions of the plankton species was significantly dependent on the amounts of dispersive and advective mass transfer. The spatial distribution in general followed the shape of an asymmetrical peak with an oscillating amplitude if limit cycles are present. If the original model predicted the convergence to a stable equilibrium solution the amplitude remained constant, see figure 3.19. The location of the peak of the asymmetrical peak moves down the river when the flow speed v of the river is increased, see figure 3.13. The width of the asymmetrical peak increases when there is more dispersive or advective mass transfer present, see figures 3.7 and 3.18.

To summarize, for the systems (3.4.1-3.4.3) considered with the spatial context of a flowing river, with dispersive and advective mass transfer, it was found that the biodiversity was still primarily dependent on the parameters present in the original model, if the conditions, mentioned in the previous paragraph, are met. This implies that a coexistence between certain species found in the original model is an indicator if that coexistence is also possible in the context of a flowing river under certain conditions regarding dispersive and advective mass transfer.

Furthermore, it was found that the paradox of plankton also appears when light intensity is added to the chemostat model (2.2-2.3). From the simulations, it was found that the total biomass and biodiversity increases as the light intensity increases. When the plankton species have insufficient amounts of light intensity the paradox of plankton disappears, either due to an increasing depth of the system or plankton species having to consume more light intensity. It was also observed, see figure 3.24, that a dominant species can be introduced if it is more efficient at consuming light intensity than the other plankton species in a system.

When the physical context and light intensity were both incorporated into the original model, it was found that in a section of the river with less clear water the spatial distribution will have a decreased amplitude in that region, but it does not significantly affect the coexistence of the plankton species in that region as long as no plankton species is better at consuming light intensity than the other. Furthermore, when a shallower region is present in the river, the plankton species were found to spent less time there due to the increased flow speed, and not experiencing a significant change in population size due to spending less time in the shallow region.

Recommendations for future research

There are several worthwhile things that future research can focus on.

First, one of the main drawback of the chemostat model is that it is challenging to verify whether the observed oscillations in figures as (3.15) are also found in real-world data. This is due to experimental data including noise from external factors, such as seasonal temperature differences and day and night cycles, which makes the low-amplitude oscillations in certain systems go unnoticed, see figure 2.10 (Huisman & Weissing, 1999). Therefore, in experimental data, there are oscillations present with bigger amplitudes, similar to the results seen in figure (3.5), that are not caused by the competition between plankton species. Future research could attempt to obtain more data from an experimental setup recreating the original chemostat model (2.1). However, it is noted that recent experimental data has been found for a system, with two resource types and two plankton species, that characteristically agrees with the simulations shown in figures 2.3, 2.4 and 2.5 (Felpeto et al., 2017). Additionally, the limit cycles that appear when the paradox of plankton exists can have a wide range of frequencies, as shown in figure 3.21.

Second, in the simulations several undesired heteroclinic cycles were found. These cycle are physically inaccurate and do not describe a realistic coexistence due to the population size of the plankton species growing infinitesimally small. This implies that the original model (2.2-2.3) lacks the inclusion of a process that prevents these heteroclinic cycles from appearing. Furthermore, it was found that certain parameter variations (2.1) could transform these heteroclinic cycles into limit cycles, which do allow for more realistic coexistence. Future research could look into the specific conditions for which heteroclinic cycles and limit cycles appear and attempt to incorporate a physical process in the original model that prevents these heteroclinic cycles from appearing. These could then be further used to inform which species can coexist in a system.

Third, in the original chemostat model it is assumed that the system is well-mixed. This has a consequence that when a new plankton species is added to the model it is assumed to be instantly homogeneously added to the system, which is unrealistic. In more realistic systems a new species is added by a local turbulence which gradually spreads into the system. Future research can try to include this behaviour by using the model described in section (3.3) and introducing a new plankton species along a specific location in the river.

Fourth, future research can attempt to change the original chemostat model to recreate the behaviour of ecosystems different than the phytoplankton community considered in this paper. The most significant assumption of the chemostat model is that the development of plankton species over time is spatially invariant, due to the population size of a plankton community the specific location of a plankton in the bioreactor has no influence, and that dying plankton get converted to resources that other plankton can not consume. Furthermore, the current model only considers resource competition, however, in other ecosystems, there is also prey-predator competition that can be incorporated.

Fifth, it was shown in section (2.4.5) how an asymptotically stable equilibrium solution may exist that has a region of convergence not equal to the domain of the system. In all other parts in this report it is assumed that an asymptotically stable equilibrium solution has a region of convergence equal to the domain of the system. However, the issue remains that the principle of competitive exclusion can sometimes be disregarded due to the simulation variables managing to avoid intersecting with the region of convergence, this is an indicator for the fragility of the ecosystem as shown in section (2.4.5). Future research can attempt to analyze which factors affect size and shape of the region of convergence and how, by carefully selecting initial values, intersecting with a region of convergence can be avoided.

Sixth, in the expansion of the original model where light intensity was incorporated, see equation (3.7), it was assumed that the plankton species were homogeneously distributed over the depth of the system. However, in reality there is a higher density of plankton at the surface of the system (Nelson, 2012). Future research can attempt to incorporate a heterogeneous distribution of plankton species over the depth of the system.

Finally, this report has given a condition for which the upper limit on biodiversity, due to the principle of competitive exclusion, can be disregarded. However, no condition is known that guarantees the existence of the paradox of plankton. There exists other dynamics in the chemostat model that can make certain species go extinct, regardless of the principle of competitive exclusion. Future research could attempt to find conditions that guarantee the existence of the paradox of plankton.

Appendix A

Model parameters

These are the model parameters for the examples given in section (2.4.4) and section (2.4.5). For the matrix K and c, the values K_{ji} and c_{ji} are the values in the j-th row and i-th column of each respective matrix. The vector N_{init} and R_{init} describe the initial values of the plankton species and resource types. The vector $N_{introduced}$ indicates at which time every plankton species is introduced to the system. The model parameters for the system with three resource types and five plankton species shown in section (2.4.4) are (Huisman & Weissing, 1999):

D	0.25
S_1	6
S_2	10
S_3	14
m_1	0.25
m_2	0.25
m_3	0.25
m_4	0.25
m_5	0.25
r_1	1.00
r_2	1.00
r_3	1.00
r_4	1.00
r_5	1.00

$$K = \begin{bmatrix} 1.00 & 0.90 & 0.30 & 1.04 & 0.34 \\ 0.30 & 1.00 & 0.90 & 0.71 & 1.02 \\ 0.90 & 0.25 & 1.00 & 0.46 & 0.34 \end{bmatrix}$$

$$c = \begin{bmatrix} 0.04 & 0.07 & 0.04 & 0.10 & 0.03 \\ 0.08 & 0.08 & 0.10 & 0.10 & 0.05 \\ 0.14 & 0.10 & 0.10 & 0.16 & 0.06 \end{bmatrix}$$

$$R_{init} = \begin{bmatrix} R_1 & R_2 & R_3 \end{bmatrix} = \begin{bmatrix} 6 & 10 & 14 \end{bmatrix}$$

$$N_{init} = \begin{bmatrix} N_1 & N_2 & N_3 & N_4 & N_5 \end{bmatrix} = \begin{bmatrix} 0.01 & 0.02 & 0.03 & 0.01 & 0.01 \end{bmatrix}$$

$$N_{introduced} = \begin{bmatrix} N_1 & N_2 & N_3 & N_4 & N_5 \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & 1000 & 2000 \end{bmatrix}$$

The model parameters for the system with three resource types and nine plankton species shown in section (2.4.5) are (Huisman & Weissing, 1999):

D	0.25
S_1	10
S_2	10
S_3	10
m_1	0.25
m_2	0.25
m_3	0.25
m_4	0.25
m_5	0.25
m_6	0.25
m_7	0.25
m_8	0.25
m_9	0.25
r_1	1.00
r_2	1.00
r_3	1.00
r_4	1.00
r_5	1.00
r_6	1.00
r_7	1.00
r_8	1.00
r_9	1.00

$$K = \begin{bmatrix} 1.00 & 0.75 & 0.25 & 0.70 & 0.20 & 0.65 & 0.68 & 0.38 & 0.46 \\ 0.25 & 1.00 & 0.75 & 0.20 & 1.01 & 0.55 & 0.83 & 1.10 & 0.85 \\ 0.75 & 0.25 & 1.00 & 1.10 & 0.70 & 0.95 & 0.60 & 0.50 & 0.77 \end{bmatrix}$$

$$c = \begin{bmatrix} 0.10 & 0.20 & 0.15 & 0.05 & 0.01 & 0.40 & 0.30 & 0.20 & 0.25 \\ 0.15 & 0.10 & 0.20 & 0.15 & 0.30 & 0.35 & 0.25 & 0.02 & 0.35 \\ 0.20 & 0.15 & 0.10 & 0.25 & 0.05 & 0.20 & 0.40 & 0.15 & 0.10 \end{bmatrix}$$

$$R_{init} = \begin{bmatrix} R_1 & R_2 & R_3 \end{bmatrix} = \begin{bmatrix} 10 & 10 & 10 \end{bmatrix}$$

$$N_{init} = \begin{bmatrix} N_1 & N_2 & N_3 & N_4 & N_5 & N_6 & N_7 & N_8 & N_9 \end{bmatrix}$$

$$= \begin{bmatrix} 0.11 & 0.12 & 0.13 & 0.10 & 0.10 & 0.10 & 0.10 & 0.10 & 0.10 \end{bmatrix}$$

$$N_{introduced} = \begin{bmatrix} N_1 & N_2 & N_3 & N_4 & N_5 & N_6 & N_7 & N_8 & N_9 \end{bmatrix}$$

$$= \begin{bmatrix} 0 & 0 & 0 & 250 & 500 & 750 & 1000 & 1250 & 1500 \end{bmatrix}$$

Appendix B

Equilibrium solution finding algorithm

```
"""
Algorithm to find all equilibrium solutions of the chemostat model:
Specify the model's parameters below. The parameters for the system with
nine plankton species and three resource types (Huisman & Weissing, 1999)
have already been filled in.
The algorithm will find all equilibrium solutions and their associated stability.
"""
from itertools import chain, combinations, permutations
import numpy as np

k = 3 # Amount of resource types
n = 9 # Amount of plankton species
# Half-saturation constants
K = [[1.00, 0.75, 0.25, 0.70, 0.20, 0.65, 0.68, 0.38, 0.46],
     [0.25, 1.00, 0.75, 0.20, 1.01, 0.55, 0.83, 1.10, 0.85],
     [0.75, 0.25, 1.00, 1.10, 0.70, 0.95, 0.60, 0.50, 0.77]]
# The amount of every resource contained in every plankton species
C = [[0.10, 0.20, 0.15, 0.05, 0.01, 0.40, 0.30, 0.20, 0.25],
     [0.15, 0.10, 0.20, 0.15, 0.30, 0.35, 0.25, 0.02, 0.35],
     [0.20, 0.15, 0.10, 0.25, 0.05, 0.20, 0.40, 0.15, 0.10]]
r = [1.00, 1.00, 1.00, 1.00, 1.00, 1.00, 1.00, 1.00, 1.00] # Growth rates
m = [0.25, 0.25, 0.25, 0.25, 0.25, 0.25, 0.25, 0.25, 0.25] # Mortality rates
D = 0.25 # Turnover rate
S = [10, 10, 10] # Supply of every resource

solutions = []

def mu(ind, resources):
    mu_list = []
    for i in range(0, len(resources)):
        mu_list.append( ( r[ind] * resources[i] ) / ( K[i][ind] + resources[i] ) )
    return min(mu_list)

def mu_index(ind, resources):
    index = 0
    value = ( r[ind] * resources[index] ) / ( K[index][ind] + resources[index] )
    for i in range(1, len(resources)):
        temp_value = ( r[ind] * resources[i] ) / ( K[i][ind] + resources[i] )
        if temp_value < value:
            value = temp_value
            index = i
    return index

def calculate_all_derivatives(resources, populations):
    populations_derivatives = []
    resources_derivatives = []
    for i in range(0, len(populations)):
        populations_derivatives.append( populations[i] * ( mu(i, resources) - m[i] ) )

    for j in range(0, len(resources)):
        total = 0
        for i in range(0, len(populations)):
            total = total + C[j][i] * mu(i, resources) * populations[i]

        resources_derivatives.append( D * ( S[j] - resources[j] ) - total )

    print( "Populations derivatives: ")
    print( populations_derivatives )
```

```python
    print( "Resources derivatives: ")
    print( resources_derivatives )

    epsilon = 1e-10
    if all(abs(i) <= epsilon for i in populations_derivatives) and all(abs(i) <= epsilon for i in resources_derivatives):
        print("Valid equilibrium point!")

def calculate_all_eigenvalues(resources, populations):
    J = []

    mu_indices = []
    for i in range(0, n):
        mu_indices.append( mu_index(i, resources) )

    for i in range(0, n):
        J_row = [0] * n
        J_row[i] = mu(i, resources) - m[i]

        for j in range(0, k):
            if mu_indices[i] == j:
                J_row.append( populations[i] * r[i] * K[j][i] / ( ( K[j][i] + resources[j] )**2 ) )
            else:
                J_row.append(0)

        J.append(J_row)

    for j in range(0, k):
        J_row = []
        for i in range(0, n):
            J_row.append(-C[j][i] * mu(i, resources) )

        for res_j in range(0, k):
            der_val = 0

            for i in range(0, n):
                if mu_indices[i] == res_j:
                    der_val = der_val - C[j][i] * populations[i] * r[i] * K[res_j][i] / ( ( K[res_j][i] + resources[res_j] )**2 )

            if res_j == j:
                der_val = der_val - D

            J_row.append(der_val)


        J.append(J_row)

    J = np.array(J)
    eigs = np.linalg.eigvals(J)
    print("Eigenvalues:")
    for eig in eigs:
        print(eig)
    epsilon = 1e-10
    if all(i < epsilon for i in eigs):
        print("Stable equilibrium point!")

    if all(i > epsilon for i in eigs):
        print("Unstable equilibrium point!")

    if any(i > epsilon for i in eigs) and any(i < epsilon for i in eigs):
        print("Unstable saddle equilibrium point!")

    if all(abs(i) < epsilon for i in eigs):
        print("Stable neutral equilibrium point!")

    if any(abs(i.imag) >= epsilon for i in eigs):
        print("Also has oscillations!")
```

```
def powerset(iterable):
    ”powerset([1,2,3]) --> [() (1,) (2,) (3,) (1,2) (1,3) (2,3) (1,2,3)]”
    s = list(iterable)
    l = []
    for el in  list(chain.from_iterable(combinations(s, r) for r in range(len(s)+1))):
        l.append(list(el))

    return l

powset = powerset(range(0,n))

#First calculate the trivial equilibrium solution
pops = [0] * n
resources = S
solutions.append({’N’: pops, ’R’: resources})
print(”Resources: ”)
print(resources)
print(”Populations: ”)
print(pops)
calculate_all_derivatives(resources, pops)
calculate_all_eigenvalues(resources, pops)
print(”---”)

#In this loop find all other potential equilibrium solutions
for el in powset:
    w = len(el)
    if w == 0:
        continue

    for p in permutations(range(0, k), w):
        q = list(p)
        B_ = [0] * w
        C_ = []

        for j in range(0, w):
            C_.append([0] * w)

        for i in range(0, w):
            ind = el[i]
            q_ind = q[i]

            B_[i] = S[q_ind] - ( m[ind] * K[q_ind][ind]) / ( r[ind] - m[ind])
            for j in range(0, w):
                ind_ = el[j]
                C_[i][j] = C[q_ind][ind_] * m[ind_] / D

        B_ = np.array(B_)
        C_ = np.array(C_)

        try:
            N_ = np.dot( np.linalg.inv(C_), B_ )
        except:
            continue

        pops = [0] * n
        for i in range(0, len(N_)):
            ind = el[i]
            pops[ind] = N_[i]

        # Positivity condition
        if all(i >= 0 for i in pops):

            resources = [0] * k

            for j in range(0, k):
                total = 0
                for i in range(0, n):
                    total = total + (1/D)*C[j][i]*m[i]*pops[i]
                resources[j] = S[j] - total

            # Positivity condition
```

```
            if all(i >= 0 for i in resources):
                check = True
                for i in range(0, w):

                    # Minimization condition
                    if mu_index(el[i], resources) != q[i]:
                        check = False
                        break

                if check:
                    solutions.append({’N’: pops, ’R’: resources})
                    print(”Resources: ”)
                    print(resources)
                    print(”Populations: ”)
                    print(pops)
                    calculate_all_derivatives(resources, pops)
                    calculate_all_eigenvalues(resources, pops)
                    print(”---”)
```

References

[1] D.R. Easterling et al. “Climate Extremes: Observations, Modeling, and Impacts”. In: *Science* 289 (2000).

[2] E. Bestion et al. “Phytoplankton biodiversity is more important for ecosystem functioning in highly variable thermal environments”. In: *The Proceedings of the National Academy of Sciences* 118 (2021).

[3] L.A. Arteaga et al. “Seasonal modulation of phytoplankton biomass in the Southern Ocean”. In: *Nature Communications* 11 (2020).

[4] T. Brown. *Plankton*. 2022. URL: `https://education.nationalgeographic.org/resource/plankton`.

[5] A.B. Felpeto, S. Roy, and V.M. Vasconcelos. “Allelopathy prevents competitive exclusion and promotes phytoplankton biodiversity”. In: *Oikos* 127 (2017).

[6] J.P. Grover. *Resource Competition*. Springer, 1997.

[7] S.A. Henson et al. “Future phytoplankton diversity in a changing climate”. In: *Nature Communications* 12 (2021).

[8] J. Huisman and F.J. Weissing. “Biodiversity of plankton by species oscillations and chaos”. In: *Nature* 402 (1999), pp. 407–410.

[9] J. Huisman and F.J. Weissing. “Oscillations and chaos generated by competition for interactively essential resources”. In: *Ecological Research* 17 (2002b), pp. 175–181.

[10] J. Huisman et al. “Principles of the light-limited chemostat: Theory and ecological applications”. In: *Antonie van Leeuwenhoek* 81 (2002a), pp. 117–133.

[11] G.E. Hutchinson. “The Paradox of the Plankton”. In: *The American Naturalist* 95 (1961), pp. 137–145.

[12] G. Lawton. “Kleine groene indringers”. In: *New Scientist* (2021). URL: `https://www.newscientist.nl/blogs/kleine-groene-indringers/`.

[13] R. Levins. “Coexistence in a Variable Environment”. In: *The American Naturalist* 114 (1979).

[14] J. Von Liebig. *Die organische Chemie in ihrer Anwendung auf Agrikultur und Physiologie*. 1840.

[15] Y. Mrabet. *Simple schematic of a bioreactor in chemostat mode*. 2009. URL: `https://commons.wikimedia.org/wiki/File:Chemostat_shematic.svg`.

[16] R. Mudde and H.E.A. van den Akker. *Fysische Transportverschijnselen*. Delft University Press, 1998.

[17] D. Nelson. *Save the Plankton, Breathe Freely*. 2012. URL: `https://www.nationalgeographic.org/activity/save-the-plankton-breathe-freely`.

[18] A. Palacios. *Heteroclinic cycles*. 2007. URL: `http://www.scholarpedia.org/article/Heteroclinic_cycles`.

[19] J. Rauch. *Asymptotic Stability by Linearization*. 2014. URL: `https://dept.math.lsa.umich.edu/~rauch/558/decreasingquadraticform.pdf`.

[20] C.S. Reynolds, J. Padisak, and U.Sommer. “Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis”. In: *Hydrobiologia* 249 (1993), pp. 183–188.

[21] P. Richerson, R. Armstrong, and C.R. Goldman. “Contemporaneous disequilibrium, a new hypothesis to explain the ”paradox of the plankton””. In: *Proc Natl Acad Sci USA* (1970).

[22] D. Tilman. *Resource Competition and Community Structure*. 1982.

[23] C. Vuik et al. *Numerical Methods for Ordinary Differential Equations*. Delft Academic Press, 2015.