The Role of Functional Traits and Trade-offs in Seasonal Succession of Phytoplankton Community Structuring:

A numerical investigation of resource acquisition traits of Lake Constance

Ayesha Nagahage
Abstract

Long-term ecological research in deep lakes offers valuable insights into understanding changes in trophic states and organization of phytoplankton assemblages. Utilizing five decades of phytoplankton taxonomic trait data from pre-alpine Lake Constance, a confirmed negative relationship was found between phosphate and light affinity at the annual community trait level. Drawing inspiration from the stronger community-level tradeoff observed between the affinity for phosphate and light among phytoplankton species in Lake Constance, I hypothesized that resource acquisition traits, characterized by the half-saturation constants for nutrient-limited growth ($M_i$) and light-limited growth ($H_i$), should exhibit a negative trade-off mechanism at the community mean trait level, derived from the traits of the species in Lake Constance. The developed model was parametrized using empirical data from the lake. Intra- and inter-annual variation in environmental conditions were incorporated in the model by considering seasonal changes in temperature, light intensity, temperature-influenced exchange rates of the vertical water column, and decadal changes in nutrients in Lake Constance. Simulations reflected observed seasonal dominance patterns of phytoplankton species and predicted differences in relative abundance under varying nutrient supplies, aligning with resource limitation trends. Consistent with empirical observations, a negative relationship between light and phosphorous affinity is observed in the 60-year simulation of Lake Constance. The elucidation of such a trade-off mechanism is expected to facilitate the understanding of the coexistence of phytoplankton species in Lake Constance amidst the decadal changes in phosphorus loading by selecting for higher light affinity during eutrophic phases and higher phosphorus affinity during oligotrophic phases.

Keywords: Phytoplankton, resource acquisition, traits, trade-off, resource limitation
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1. Introduction

The concept of natural selection, whereby species evolve through modifications to better adapt to their natural environment, emerged with Charles Darwin's theory in 1859. It has since enriched biology and serves as a fundamental tool for comprehending how traits evolve in a correlated fashion with trade-offs (Garland, 2014). In recent decades, significant strides have been made in the field of trait-based community ecology, primarily focused on terrestrial plant systems, to elucidate the intricate processes governing community structuring. While these studies have provided valuable insights, there is a growing interest in extending trait-based approaches to elucidate the dynamics of freshwater and marine phytoplankton ecosystems, particularly in the context of global environmental changes (Dory et al., 2023; Edwards et al., 2013a; Litchman & Klausmeier, 2008) and trophic states changes (Carpenter, 2005; Jochimsen et al., 2013; Schwaderer et al., 2011) by human development activities. Given that phytoplankton serve as the dominant primary producers, accounting for nearly half of the Earth’s primary productivity (Field et al. 1998) also their community composition exerts a profound influence on the trophic dynamics of aquatic ecosystems (Sterner & Elser, 2002) and water quality (Anderson et al., 1998). Therefore, gaining a comprehensive understanding, precise description, and accurate forecasting of the dynamics driven by environmental variables in these pivotal ecosystems become imperative for scientific inquiry and ecosystem management.

Field and laboratory-based studies of marine and freshwater ecosystems have consistently demonstrated that a complex interplay of biotic, abiotic, and environmental factors, encompassing elements such as nitrogen, phosphorus, silica, iron, light, temperature, and grazers, exerts a significant influence on the composition of phytoplankton communities (Johnson et al., 2006; Landry et al., 2000; Stomp et al., 2007; Tilman et al., 1982). These characteristics or attributes, expressed by genes and influenced by the environment, are measurable and can be used as functional traits to understand the interactions between species. Litchman and Klausmeier (2008) introduced a comprehensive typology of phytoplankton traits, which encompasses a wide range of characteristics, including life history (e.g., reproduction and resting stages), behavioral patterns, physiological features, and morphological traits. These diverse traits collectively serve essential ecological functions, namely reproduction, resource acquisition, and predator avoidance. Resource acquisition, utilization, and defense mechanisms can be discerned through the comprehensive analysis of traits and trait trade-offs within phytoplankton communities. The identification of mechanistic features of functional traits is accelerated within phytoplankton communities, owing to their rapid trait expression.

Previous trait-based studies on phytoplankton communities in various lakes and marine ecosystems have been helpful in identifying common trade-off patterns, including trade-offs between defense and growth traits (Ehrlich et al., 2020) and between resource acquisition and utilization traits (Edwards et al., 2013a; Edwards et al., 2013b; Smith et al., 2009; Stomp et al., 2007). Among these patterns, resource utilization and competition for resources play pivotal roles (Tilman, 1982; Button, 1985; Hibbing et al., 2010), significantly influencing trophic state dynamics in both marine and freshwater ecosystems. Consequently, there is growing interest within the scientific community in understanding the mechanisms underlying community structuring. The relationship between growth rate and resource availability, such as light or nutrients, can be mathematically described using Monod equations (multiplicative Monod terms in Equation 3), with parameters such as half-saturation constants for phosphate $M_i$ and light $H_i$ serving as measurable traits for different phytoplankton species. It is because different
phytoplankton groups and individual species respond differently to light (Richardson et al. 1983) and changing nutrients (Carpenter, 2005; Jochimsen et al., 2013; Schwaderer et al., 2011). Thus, to comprehend how light and nutrients shape the phytoplankton community, a comprehensive understanding of the phytoplankton traits associated with both light and nutrient utilization is essential. Importantly, these diverse traits are quantifiable in both laboratory experiments and field assessments, facilitating the parameterization of predictions for phytoplankton population dynamics (Grover, 1991; Passarge et al., 2006; Schwaderer et al., 2011; Tilman, 1977).

In the trait-based approach, community mean trait analysis has been introduced to investigate the relationship between environmental factors and community composition. Building upon this approach, in a previous study conducted by Pranger et al. in 2023 (unpublished manuscript), a negative relationship was empirically validated between the affinity for phosphate and light at the level of the annually averaged community traits, by analyzing a 42-year time series from Lake Constance that covered large changes in external phosphorus loading. The inferred tradeoff between the affinities for phosphate and light was stronger at the community level but appeared weaker at the species level. Building upon Pranger et al.’s study, I hypothesized that the negative trade-off between the half-saturation constants for nutrient- vs. light-limited growth that was observed at the level of community mean traits can be derived from the traits of the species present in Lake Constance, selecting for higher light affinity during eutrophic phases and higher phosphorus affinity during oligotrophic phases. To investigate the plausibility of this hypothesis, I used a dynamical modelling approach in which I exposed a set of phytoplankton species that share a common trade-off between light and phosphorus affinity to changes in environmental conditions that mimicked the changes in phosphorus loading observed in Lake Constance.

2. Materials and Methods

2.1 Empirical data used to parameterize and validate the model

The empirical data that I used for my numerical investigation were collected in the upper 20 m of the pelagic zone of Lake Constance, a deep (max. depth 250m), monomictic, pre-alpine lake bordered by Germany, Switzerland and Austria. The lake consists of a well-mixed epilimnion and a large pelagic zone (Gaedke et al., 2002). The 42-years of measured data during the period from 1966-2007 cover the trophic change of Lake Constance from eutrophic to reeoligotrophic conditions. The total phosphorous concentration declined four-fold from 1979 to 1996 resulting annual phytoplankton biomass and production decline by 50 and 25%, respectively (Gaedke, 1998).

In my investigation, I examined the resource acquisition traits phosphate and light affinity to provide a reasonable explanation for the trophic changes observed in Lake Constance. During the study period of Lake Constance, water samples covering the depth range 0-20 m were taken at approximately bi-weekly intervals at station Fischbach-Utwill. A detailed description of phytoplankton sampling and biovolume estimation is found in Jochimsen et al. (2013). Out of a total of 27 different phytoplankton classes, the six most abundant classes, i.e. Cryptophyceae, Mediophyceae (polar centric diatoms), Bacillariophyceae (penate diatoms), Dinophyceae, Chlorophyceae and Cyanophyceae, contributed about 90% to the annual mean community biovolume (summed over all taxa with cell volumes >30 μm³).
2.2 Model formulation

The model structure consisted of two differential equations, one describing phytoplankton biomass and the other describing mineral nutrient dynamics within a vertically well-mixed layer of 20 m depth. Additionally, an algebraic equation describes the vertical attenuation of incident light in the water column. To parametrize the model, empirical data from Lake Constance were employed. The detailed model components of the model include temperature-dependent functions describing growth and losses of biomass, remineralization, etc. as elaborated in subsequent sections. The intra- and inter-annual variation of environmental conditions was incorporated through considering relevant changes in temperature, light intensity, temperature-influenced exchange rates of the vertical water column, and decadal changes in nutrients in Lake Constance. These environmental processes were mainly described by trigonometric functions. The hydrodynamic and mechanistic status of the vertical mixing layer, influenced by environmental drivers, are explained in detail below.

2.2.1 Model structure

The model is designed to depict the competitive interactions among different algal species $A_i$ in the well-mixed surface layer of a lake in their competition for two limiting resources: nutrients ($R$) and light ($I$). The dynamically changing phytoplankton system is described by two types of differential equations: a set of $i$ equations describing the production and losses of the biomass of $i$ species of phytoplankton ($\frac{dA_i}{dt}$) and one equation describing nutrient gain and depletion ($\frac{dR}{dt}$) in the water column. In addition, vertical light attenuation is described by an algebraic equation, yielding

Eq. 1a \[ \frac{dA_i}{dt} = I_m + \frac{A_i}{z} \int_0^z p(I(s),R) - (I(T) + D)A_i \]

Eq. 1b \[ \frac{dR}{dt} = D(R_{in} - R) + qf(I(T)\sum A_i - q \frac{A_i}{z} \int_0^z p(I(s),R) \]

Eq. 1c \[ I(s) = I_{in}(t)\exp \left(-s(K_{bg} + k\sum A_i) \right) \]

All state variables and parameters are defined with their units in Table 1. The rate of change of the biomass of phytoplankton species $i$, $\frac{dA_i}{dt}$, considers the gains and losses of phytoplankton biomass in a one-dimensional vertical water column of depth $z$, which is assumed to be well-mixed. The gains include light and nutrient limited production $p(I(s),R)$ and a very small, constant immigration rate ($I_m$) mimicking recruitment from resting stages. The losses $l$ include biological processes such as respiration, pathogens, grazing activity, diseases, etc. as well as advection to deeper, aphotic layers at rate $D$ (Equation 1a). The seasonal fluctuations in exchange rates, attributed to changes in thermal stratification of the lake, result in shifts of the nutrient influx from deep water into the upper part of the water column. The rate of change of the limiting nutrient, $\frac{dR}{dt}$, considers nutrient received through upward transport from deeper, aphotic layers at rate $D$ and from the re-mineralization of a certain fraction $f$ of the algal biomass losses $l$ as well as nutrient uptake related to phytoplankton production (Equation 1b). Light availability exhibits an exponential decrease with increasing depth $s$ in the water column following Lambert-Beer’s law, characterized by the specific light attenuation coefficient of algal biomass ($k$) and the background attenuation coefficient of the water medium ($K_{bg}$) (Equation 1c).
The term \( p(I(s), R) \) in Equation 1a, is the specific rate of algal production as a function of light intensity at depth \( s \) and nutrient availability, where \( p_{\text{max}} \) is the maximum growth rate at fully saturating resource levels. Building upon the theoretical framework presented by Huisman and Weissing (1995) and the previous work by Diehl (2002) and Jäger and Diehl (2014), I employ an assumption that the resource dependence of algal growth with respect to nutrients \( (R) \) and light \( (I) \) can be mathematically expressed as two multiplicative Monod terms:

Eq. 2  
\[
p(I(s), R) = p_{\text{max}} \left[ \frac{I(s)}{H_i + I(s)} \cdot \frac{R}{M_i + R} \right]
\]

The integral in Equations 1a and 1b can be solved following Huisman and Weissing (1995) and Gurney et al. (1998) as

Eq. 3  
\[
\int_0^z p(I(s), R) \, ds = p_{\text{max}} \int_0^z \frac{I(s)}{H_i + I(s)} \, ds \cdot \frac{R}{M_i + R} = \frac{p_{\text{max}}}{K_B + k \sum_i A_i} \cdot \ln \left( \frac{H_i + I_{\text{in}}}{H_i + I(z)} \right) \cdot \frac{R}{M_i + R}
\]

In Equations 1a, 1b and 3, \( I(s) \) is the light intensity at depth of \( s \), which is integrated from the surface \( (s = 0) \) to the bottom of the mixed water column \( (s = z) \).

### 2.2.2 Parametrization of resource acquisition traits

The empirical data for resource acquisition traits from Pranger et al.’s 2023 study, i.e. the phosphate affinities \( a_{pi} \) and light affinities \( a_{li} \) of phytoplankton species \( i \), were further transformed into the half-saturation constants for nutrient-limited growth \( (M_i) \) and light-limited growth \( (H_i) \), calculated using Equation 4 and Equation 5, respectively.

Eq. 4  
\[
M_i = \frac{p_{\text{max}}}{a_{pi}}
\]

Eq. 5  
\[
H_i = \frac{p_{\text{max}}}{a_{li}}
\]

Finally, to ensure that our parameterization of the half saturation constants \( H_i \) and \( M_i \) for light and nutrient dependent growth, respectively, followed the empirically observed trade-off between the light and phosphate affinities of the species in Lake Constance, we translated this relationship (i.e., \( a_l = 1 \times 10^{-6} a_p^{0.504} \)) into a corresponding power function in terms of the half saturation constants, \( H_i = 20.93 M_i^{-0.504} \) (Fig. 1).
2.2.3 Temperature dependence of growth and loss rates

I assume a seasonality-dependent temperature effect on the maximum specific growth rate of phytoplankton as described in eq. 6.

\[ P_{\text{max}}(T) = P_0 \exp(\alpha T) \]

In this equation, \( T \) is temperature (in °C), the parameter \( \alpha \) is the coefficient governing the temperature dependence of algal growth, and \( P_0 \) is the maximum specific production rate that a particular species can reach at a reference temperature of 0°C. In my study, these parameters were held constant across all algal species.

Background losses \( l \), which include respiration losses and mortality/losses due to factors such as grazing and diseases, were assumed to be considerably lower than \( P_{\text{max}} \) but to otherwise follow a similar exponential relationship with temperature as described in eq. 6 (i.e. the parameter \( \alpha \) has the same value, Fig. 2). To maintain consistency with previous work, I selected the value of \( l_0 \) to achieve a standard background loss rate of \( l = 0.1 \) at 20 degrees Celsius (Fahnenstiel, G. L.; Michael J. McCormick, 1995; Kiorboe T.; Hansen, 1996). In my model, a portion of these background losses contributes to nutrient recycling. For instance, in the case of algal background respiration, some nutrients may be excreted. Similarly, grazers that feed on algae often do not assimilate all the ingested nutrients and excrete some as well. This concept also applies to disease dynamics, where viral lysis can lead to nutrient recycling. The term \( q * f * l * A_i \) in the equation for \( dR/dt \) accounts for this nutrient recycling process, where \( l \) denotes the algal loss rate, \( f \) represents the fraction of lost biomass that is recycled, and \( q \) stands for the nutrient content within the algal biomass. For this model, I have chosen \( f = 0.5 \), indicating a 50% recycling rate. It is important to note that the choice of 50% recycling is somewhat arbitrary, but it provides a reasonable starting point for my simulations.

\[ l(T) = l_0 \exp(\alpha T) \]
The model assumes that all phytoplankton species have identical traits (i.e. share identical parameters) with the exception of their half-saturation constants for nutrients and light dependent growth. Seasonal variation in various environmental conditions (incident light, temperature and water exchange with between surface and deep water) was introduced to the model as explained in the following section.

2.2.4 Seasonal and inter-annually changing environmental drivers

For the model parameterization, I acquired data on the annual temperature fluctuations at different depths in Lake Constance from the Institute for Lake Research (ISF) at the Baden-Württemberg State Institute for the Environment (LUBW, Germany). Additionally, annual radiation data (in Wm$^{-2}$) for Lake Constance were obtained from the Swiss Meteorological Department (Meteo Swiss, Switzerland). These annual radiation data were converted to photosynthetically active radiation (PAR) by assuming that 50% of solar radiation is PAR and that PAR energy converts to photon flux density as 4.56 $\mu$mol photons s$^{-1}$ W$^{-1}$ (McCree, 1972).

Physical environmental drivers play a vital role in shaping the phytoplankton community in a lake ecosystem. In response to the seasonal fluctuation in temperature, light, and the exchange rate between surface and deep water, both the nutrient transport to the surface water and the loss rate of phytoplankton to aphotic depth increase or decrease in different seasons of the year. In Lake Constance, stable stratification prevails from April to November, while the entire water column is approximately homothermic during the rest of the year, leading to a complete overturn (Sommer, 1985). The resulting abrupt shifts in the water and nutrient exchange rate during transitions between overturn and stratification, as well as the more subtle and continuous shifts in water exchange caused by changes in temperature during periods of stratification can be described by the combination of a square wave with a sinusoidal function (Equation 8).
I carefully selected appropriate exchange rate values to parameterize this function. The surface water experiences significant seasonal variations in mixing dynamics, with strong mixing in the winter (exchange rate, $D$, approximately 0.6 per day) and weak mixing in the summer ($D$, approximately 0.01 per day). The transition between these two mixing regimes is notably abrupt, which cannot be adequately represented by a simple sine wave. Therefore, I devised a periodic function that combines a 'square wave' component with a sine wave. This composite function exhibits sine wave-like behavior with small amplitudes during the summer and winter but undergoes a rapid change during early spring and late fall (Fig. 3). The times of minimum and maximum values of the $D$ function correspond to the periods of highest and lowest water temperatures, aligning closely with observed data.

The seasonal changes of water temperature and incident light can be described by sinusoidal functions (Equation 9 and Equation 10 respectively).

Eq. 8 \[ D = D(t) = D_a + D_b \left( 0.8 \cdot \text{square wave} \left( \frac{2\pi}{365} t - D_c, D_d \right) \right) + 0.2 \cdot \sin \left( \frac{2\pi}{365} t - (D_c + 0.6) \right) \]

Based on meteorological data, I carefully selected the most relevant temperature and light intensity data to parameterize these functions to yield the annual trajectories shown in Fig. 3. Thus, the average annual temperature amplitude in Lake Constance ranges from 5 to 25°C, the minimum temperature occurring around day 40 (10 February) and the maximum temperature occurring around day 220 (10 August), consistent with the measured data. In similar agreement with data, incident light at the lake surface (averaged over a complete 24 hour cycle), denoted as $I_{in}$, varies on average between 90 µmol photons m$^{-2}$ s$^{-1}$ around 20 December and 590 µmol photons m$^{-2}$ s$^{-1}$ around 20 June. The values and definitions of the coefficients describing seasonal variation in incident light ($I_a, I_b, I_c$), water exchange rate ($D_a, D_b, D_c, D_d$) and surface water temperature ($T_a, T_b, T_c$) can be found in Table 1.
Figure 3. Intra-annual variation in incoming light, surface water temperature, and the exchange rate between surface water and deep water (vertical mixing) as implemented in the model simulations.

Table 1. Definitions and units of state variables and parameters, and basic set of parameter values.

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Units and basic value</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>( A_i )</td>
<td>mg C m(^{-3}) d(^{-1})</td>
<td>Phytoplankton biomass in the mixed surface layer</td>
</tr>
<tr>
<td>( a )</td>
<td>0.1</td>
<td>Coefficient of temperature dependence of algal growth</td>
</tr>
<tr>
<td>( D )</td>
<td>d(^{-1})</td>
<td>Exchange rate across the interface between the mixed layer and the deep water</td>
</tr>
<tr>
<td>( D_{ao}, D_{bo} )</td>
<td>0.3015, -0.2915</td>
<td>Coefficients of the sinusoidal-square function describing the seasonal variation in water exchange rate. They represent the vertical shift, amplitude, horizontal shift, and stratification period of the year, respectively.</td>
</tr>
<tr>
<td>( D_a, D_b, D_c )</td>
<td>0.55, 6.25</td>
<td>Coefficients of the sinusoidal function describing the seasonal changes in incident light. They represent the vertical shift, amplitude, and horizontal shift, respectively.</td>
</tr>
<tr>
<td>( f )</td>
<td>0.5</td>
<td>Fraction of recycled nutrients from algal background losses</td>
</tr>
<tr>
<td>( H_i )</td>
<td>( \mu )mol quanta m(^{-2}) s(^{-1})</td>
<td>Half saturation constant of light-limited production</td>
</tr>
<tr>
<td>( I_m )</td>
<td>( \mu )mol quanta m(^{-2}) s(^{-1})</td>
<td>Incident light intensity at the water surface</td>
</tr>
<tr>
<td>( I(z) )</td>
<td>( \mu )mol quanta m(^{-2}) s(^{-1})</td>
<td>Light intensity at the bottom of the mixed layer</td>
</tr>
<tr>
<td>( R_{ao}, R_{bo}, R_c )</td>
<td>330, -250, 4.51</td>
<td>Coefficients of the sinusoidal function describing the seasonal changes in incident light. They represent the vertical shift, amplitude, and horizontal shift, respectively.</td>
</tr>
<tr>
<td>( I_m )</td>
<td>0.1 mg C m(^{-3}) d(^{-1})</td>
<td>Immigration rate from resting stages</td>
</tr>
<tr>
<td>( k )</td>
<td>0.0003 m(^{2})/mg C</td>
<td>Specific light attenuation coefficient of biomass</td>
</tr>
<tr>
<td>( k_{bg} )</td>
<td>0.25 m(^{-1})</td>
<td>Background light attenuation coefficient</td>
</tr>
<tr>
<td>( l_0 )</td>
<td>0.013 d(^{-1})</td>
<td>Background phytoplankton loss rate at 0° Celsius</td>
</tr>
<tr>
<td>( M_i )</td>
<td>mg P m(^{-3})</td>
<td>Half saturation constant of nutrient-limited production</td>
</tr>
<tr>
<td>( P_{max} )</td>
<td>d(^{-1})</td>
<td>Maximum specific production rate of biomass</td>
</tr>
<tr>
<td>( P_0 )</td>
<td>0.2</td>
<td>Maximum specific phytoplankton production rate at 0° Celsius</td>
</tr>
<tr>
<td>( q )</td>
<td>0.02 mg P/mg C</td>
<td>Nutrient content per unit phytoplankton biomass</td>
</tr>
<tr>
<td>( R )</td>
<td>mg P m(^{-3})</td>
<td>Concentration of nutrients in the mixed surface layer</td>
</tr>
<tr>
<td>( R_m )</td>
<td>mg P m(^{-3})</td>
<td>Nutrient concentration in the deep water</td>
</tr>
<tr>
<td>( R_T )</td>
<td>mg P m(^{-3})</td>
<td>Concentration of total nutrients (= sum of mineral nutrients and nutrients in phytoplankton biomass) in the mixed surface layer</td>
</tr>
<tr>
<td>( R_{ao}, R_{bo}, R_c )</td>
<td>45, -40, 3(\pi)/2</td>
<td>Coefficients of the sinusoidal function describing the decadal-scale changes in nutrient supply to the lake. They represent the vertical shift, amplitude, and horizontal shift, respectively.</td>
</tr>
<tr>
<td>( T_{ao}, T_{bo}, T_c )</td>
<td>15, -10, 5.4</td>
<td>Coefficients of the sinusoidal function describing the seasonal changes in surface water temperature. They represent the vertical shift, amplitude, and horizontal shift, respectively.</td>
</tr>
<tr>
<td>( z )</td>
<td>20 m</td>
<td>Depth of the mixed layer</td>
</tr>
</tbody>
</table>
2.3 Numerical experiments
I performed extensive numerical experiments in which I simulated the dynamics of multiple phytoplankton species in a 20-meter deep water column over a large range of external nutrient supply levels $R_{in}$. I ran the model with different numbers of phytoplankton species, including 3, 5, 10, and 20 species, where the traits of the species were evenly spaced across the full range of half saturation trait values depicted on the trade-off line in Fig. 1. Since all of these simulations yielded very similar results, I selected the 10-species model for further analysis. This number of species was sufficient to illustrate how intra- and inter-annual changes in nutrient supply affect trait-dependent phytoplankton performance dynamics while keeping the complexity of the result interpretation low.

2.3.1 Seasonal community dynamics at different levels of nutrient supply $R_{in}$
Following the model parameterization for $M_i$ and $H_i$, the model was executed for varying nutrient concentrations by adjusting $R_{in}$ values, ranging from 1 to 100 mg P/m$^3$. The $R_{in}$ values were incremented from 1 to 10 with intervals of 1, from 12 to 20 with intervals of 2, and from 20 to 100 with intervals of 5, resulting in a total of 31 simulation runs. To generate simulation plots for low, moderate, and high nutrient concentrations, $R_{in}$ values of 6, 50, and 100 mg P/m$^3$ were employed. Subsequently, these plots were used to assess the trophic changes in the lake.

2.3.2 Inter-annual community dynamics during simulated eutrophication and re-oligotrophication
In a second numerical modelling approach, I extended the model to more closely mimic the multi-decadal time series described in Pranger et al. That study spans a period of 42 years, encompassing parts of Lake Constance’s transition from oligotrophic to eutrophic conditions as well as the major part of the period of re-oligotrophication. To capture trophic changes observed over this time scale, I extended the model to simulate the fluctuations in external nutrient supply experienced by the lake over a period of six decades, tracing its journey from oligotrophic to eutrophic conditions and back over this extended timeframe. To do so, I used a sinusoidal function that describes changes in the nutrient concentration of the deep water $R_{in}$ (Equation 11).

\[
R_{in} = R_a + R_b \cdot \sin\left(\frac{2\pi}{60\times365} t - R_c\right)
\]

This function describes the decadal-scale change in nutrient supply from oligotrophic to eutrophic conditions and back over the period from 1950 to 2010 (i.e., a time series of 60*365 daily time steps, Fig. 4).
2.3.3 Simulation outputs and comparisons with empirical data from Lake Constance

Each single simulation yielded a temporal trajectory of the concentration of dissolved phosphorus and the biomasses of all 10 species of the phytoplankton community. Simulations with temporally fixed levels of nutrient supply $R_{in}$ typically converged on the same annual trajectory already after a few weeks of the first year. I therefore ended these simulations at the end of the fifth year and used the output data from year 5 for further analyses. Output from the simulations of the 60-year time series of trophic change were used as is.

From the simulated biomass trajectories of the different phytoplankton species, I calculated the following two variables for every day of the year $t$ in the same way as Pranger et al. had done with the empirical phytoplankton data from Lake Constance: (1) the total phytoplankton biomass summed over all $n = 10$ species, $B(t) = \sum_{i=1}^{n} B_i(t)$; (2) the relative biomass of each species, $b_i(t) = B_i(t)/B(t)$. For each yearly time series $y$, I then calculated the annual mean relative biomass of each species as $b_i(y) = \sum_{j=1}^{365} b_{ij}(t)$. Calculated in that way, the annual mean relative biomasses $b_i(y)$ emphasize the average composition of the community without being dominated by blooming taxa in spring and summer and emphasize the response of the phytoplankton community to long-term changes in trophic state.

To calculate annually averaged community-level mean trait values, I computed the geometric means of all species' traits, considering their annual mean relative biomasses $b_i(y)$ as...
weighting factors. To achieve this, the following mathematical expression was employed, utilizing logarithmically transformed values for individual species:

\[ CMT(y) = \exp\left(\sum_{i=1}^{n} \ln(\tau_i) \cdot b_i(y)\right) \]

where \( CMT(y) \) is the annually averaged value of the community mean trait, \( \tau_i \) is the trait value of species \( i \), and \( b_i(y) \) is the annual mean relative biomass of species \( i \), calculated as described in the previous paragraph. Note that Pranger et al. have expressed resource acquisition traits \( \tau_i \) in terms of resource affinities rather than half saturation constants. To enable a direct comparison of our model output with Pranger et al.'s empirical observations, we used equations 4-6 to calculate community mean trait values in terms of affinities (Equations 13 and 14)

\[ CMT_{ap} = P_0 \cdot \exp\left(\sum_{i=1}^{n} (a \times 20) \cdot \ln\left(\frac{1}{M_i}\right) \cdot b_i(y)\right) \]

\[ CMT_{ai} = P_0 \cdot \exp\left(\sum_{i=1}^{n} (a \times 20) \cdot \ln\left(\frac{1}{H_i}\right) \cdot b_i(y)\right) \]

where \( a_p \) is phosphate affinity, \( a_i \) is light affinity, \( P_0 \) is the phytoplankton maximum specific growth rate at 0° Celsius, and \( a \) is the coefficient describing the temperature dependence of the maximum specific growth rate \( P_{max} \) (see Equation 6).

3. Results

3.1 Seasonal dynamics at different levels of nutrient supply \( R_{in} \)
Because environmental conditions were assumed to follow a fixed annual cycle (Fig. 3), simulated phytoplankton and resource dynamics always very quickly homed in on a seasonal trajectory that was identical year after year. At all levels of nutrient supply \( R_{in} \), this repetitive seasonal trajectory was reached already in the second year (see Appendix Fig. A1). I therefore terminated all simulations at the end of year 5 and subsequently present only data from that final year. In the following, I first describe the general seasonal trends observed in all numerical simulations, and subsequently explore how seasonal dynamics, species composition and annual mean traits of the phytoplankton community differ between simulations run at different levels of nutrient supply.

At all levels of nutrient supply \( R_{in} \), the same seasonal pattern is observed. Early in the year phytoplankton biomass is very low and dissolved phosphorus is abundant (Fig. 5), because light supply and water temperature are low and vertical mixing with more nutrient rich deep water is high (Fig. 3). These conditions prevail until increasing light supply and rising water temperatures induce thermal stratification on day 100 of the year, which was modeled as an abrupt drop in vertical mixing (Fig. 3). This drop in vertical mixing triggers a spring phytoplankton bloom, which lasts until dissolved phosphorus in the surface layer is exhausted (Fig. 5). Subsequently, phytoplankton biomass drops sharply, because low vertical mixing during summer cannot resupply the nutrients contained in the non-recycled fraction of the phytoplankton background losses (Fig. 5). Vertical mixing reaches a minimum around day 240 and subsequently increases again as water temperature starts to decline and thermal stratification is weakened (Fig. 3). This increases the resupply of dissolved phosphorus from the deep water and triggers a second phytoplankton bloom in the autumn. The autumn bloom is considerably lower than the spring bloom and ends abruptly around day 330 (Fig. 6), when thermal stratification breaks down and the lake turns over (modeled as an abrupt increase in
vertical mixing, Fig. 3). Overall, the model thus qualitatively reproduces the typical seasonal dynamics observed in a deep monomictic lake such as Lake Constance (Gaedke et al., 2002; Peeters et al., 2007).

![Figure 5](image)

**Figure 5.** Seasonal trajectories of the biomasses of phytoplankton species A1-A10 (upper row of panels), the total light attenuation coefficient (i.e., the sum of background light attenuation plus attenuation by phytoplankton biomass = $k_{bg} + k \sum_{i=1}^{10} A_i$) (middle row of panels), and the concentration of mineral phosphorus in the water column (bottom row of panels). Shown are examples of low (= 6 mg P/m$^3$, column a), intermediate (= 50 mg P/m$^3$, column b) and high (= 100 mg P/m$^3$, column c) nutrient supply in simulation year 5, when system dynamics had converged on the shown seasonal trajectories. The x-axes are scaled in units of day of the year.

With increasing nutrient supply $R_{in}$, the duration of the period of strong nutrient limitation in summer (when dissolved phosphorus concentration is close to zero) becomes shorter; consequently, phytoplankton biomass reaches higher levels both during bloom phases and in the middle of summer the higher the nutrient supply (compare across the upper row of panels in Fig. 5 and across the lower row of panels in Fig. 6). Moreover, higher phytoplankton biomass is always accompanied by higher self-shading (see middle row of panels in Fig. 5). The degree of light limitation during spring and autumn becomes therefore higher, while the period of strong nutrient limitation becomes shorter, the higher the nutrient supply $R_{in}$. Observed patterns of seasonal dominance of different phytoplankton species as well as observed differences in relative species abundance between different levels of nutrient supply are in line with these trends in resource limitation, as is described in the following paragraphs.

At all levels of nutrient supply $R_{in}$, the relative importance of light vs. nutrient limitation varies in a seasonally predictable way. During winter overturn, nutrients are abundant but incident light is low and losses due to mixing to aphotic depths are very high. Consequently, the biomasses of all species are very low during winter, and it is species A1, the species with the highest light affinity (and lowest phosphorus affinity) that benefits most from the abrupt decline in vertical mixing during the onset of stratification and always dominates the spring bloom (Fig. 5 and 6).
Subsequently, when dissolved phosphorus becomes increasingly depleted, resource limitation shifts gradually towards decreased light and increased nutrient limitation. Seasonally progressing nutrient depletion therefore facilitates the relative performance of species with increasingly higher nutrient affinities. From spring to summer, different species therefore sequentially replace each other as the temporally most abundant species in the order of their relative light and phosphate affinities (Fig. 5 and 6). Consequently, A1, the species with the highest light affinity (= best light competitor) always dominates during the spring bloom, while species with higher nutrient affinities (species A6-A10) dominate during the summer period of strong phosphorus depletion (Fig 5 and 6, see also Appendix Fig. A2).

Which of species A6-A10 will come to dominance in summer depends on overall nutrient supply $R_{in}$. At the lowest $R_{in}$, seasonal succession proceeds all the way to the superior nutrient competitor A10 (Fig. 6a), whereas at higher $R_{in}$, phytoplankton biomass and, consequently, shading by competitors is too high and the period of strong nutrient depletion is too short to sufficiently benefit species A10, and a species with intermediate competitive abilities (i.e. intermediate light and nutrient affinities) such as species A6 and A7 comes to dominance in summer (Fig. 6b and c). Conversely, as nutrient supply increases, A1’s dominance intensifies, resulting in a larger population size and a longer period of dominance of A1 at the expense of especially the weakest light competitors A9 and A10 (Fig. 6).

![Figure 6](image-url)

Figure 6. Seasonal trajectories of changes in the relative contribution to the total biomass by phytoplankton species A1-A10 (upper row of panels) and in the changes in total biomass of phytoplankton in examples of low (= 6 mg P/m$^3$, column a), intermediate (= 50 mg P/m$^3$, column b) and high (= 100 mg P/m$^3$, column c) nutrient supply. The x-axes are scaled in units of day of the year.
Figure 7. Relative contribution to the annual mean total phytoplankton biomass of species A1-A10 as a function of nutrient supply, $R_{in}$.

The influence of nutrient supply $R_{in}$ on the trait-dependent relative performances of different phytoplankton species can be visualized by looking at trends in annual mean relative biomass along a large gradient in $R_{in}$, as illustrated in Fig. 7. The figure shows that species abundances change in a systematic way along the gradient in nutrient supply. Specifically, in very nutrient poor systems ($R_{in} < 6 \text{ g P/m}^3$), the species rank in relative abundance from A10 to A1 according to their phosphate affinities, because phosphate is strongly limiting during almost the entire growing season (the part of the year when the lake is not completely mixed). Conversely, in very nutrient rich systems ($R_{in} > 140 \text{ g P/m}^3$), the species rank in relative abundance from A1 to A10 according to their light affinities, because the biomass that can build up during the spring bloom becomes extremely high and spills over into the summer. Consequently, (self-)shading is very high, and light remains the most strongly limiting resource during most of the growing season.

Figure 7 also highlights a seasonal asymmetry that favors spring bloomers with high light affinity (species A1 and A2) over summer species with high nutrient affinity (species A9 and A10) in systems with a nutrient supply of $R_{in} > 30 \text{ g P/m}^3$. The reason for this asymmetry is that spring bloomers always build a higher peak biomass than summer species, because nutrients are at their annual maximum at the onset of the spring bloom, and that dominance of the spring bloomers spills over into the summer if the nutrient pulse in the spring is sufficiently high. Note also that no species goes completely extinct in any of the simulations because we assume a small immigration from resting stages or external sources.
3.2 Inter-annual community dynamics during simulated eutrophication and re-oligotrophication

Figure 8. Intra-annual trajectories of a) the biomasses of phytoplankton species A1-A10, b) dissolved phosphorous concentration of the lake water spanning the years 1950 to 2010, reflecting the lake’s trophic states of oligotrophic, eutrophic, and re-oligotrophic as simulated by the model employed in this study.

Figure 8 illustrates the simulated changes in phosphorus concentration and phytoplankton biomass over a 60-year time span corresponding to the periods of increasing and decreasing phosphorous loading in Lake Constance. Figure 8b shows the simulated gradual increase in phosphorus concentration, peaking in the 1980s and inducing eutrophic conditions in the lake. Subsequent to this peak, phosphorus concentration gradually declines over the decades, restoring the lake to re-oligotrophic conditions. In the simulations, this results in increasing
phytoplankton biomass during the period from 1960 to 1980. Subsequently, the biomass of the phytoplankton community gradually declines as the lake transitioned from eutrophic to re-oligotrophic conditions. Importantly, the inter-annual dynamics of phytoplankton biomass demonstrate a responsive pattern corresponding to fluctuations in phosphorus concentration.

Intra-annual variations reveal a seasonal succession of the phytoplankton community, aligning with annual changes in light intensity. Within each year, distinct spring and autumn blooms are observed. Notably, the species with highest light affinity, A1, exhibits higher biomass production, dominating the spring bloom and overshadowing other species. In intra-annual variations, both A1 and A2 species exhibit the most pronounced responses to eutrophication (and re-oligotrophication). The responses to low, medium, and high phosphorous concentrations are very similar to the phytoplankton community dynamics observed in Fig. 5 for the constant, fixed $R_{in}$ values.

3.3 Relationship between nutrient supply, $R_{in}$, and community mean traits

![Graphs](image)

Figure 9. Community mean trait values for light affinity and phosphorus affinity obtained from the model simulations for varying nutrient enrichment ($R_{in}$) from 1-100 mg P/m³. (a) Community mean light affinity vs. $R_{in}$. (b) Community mean phosphorus affinity vs. $R_{in}$. (c) Community mean light affinity vs. community mean phosphorus affinity. Both x and y axes are in log transformed values. Also shown are $R^2$ values of linear regressions and the fitted regression lines.

Figure 9 summarizes the community mean trait (CMT) results obtained from a total of 31 simulation runs for phosphorus loadings, $R_{in}$, ranging from 1 to 100 mg P/m³. The results reveal a strong positive correlation with light affinity and a strong negative correlation with phosphorous affinity across various $R_{in}$ values which resulted in a perfect negative correlation ($R^2 = 1$) between community mean light and phosphorus affinities. Remarkably, the latter relationship aligned perfectly with the best-fitted empirical trait relationship that was used to define the trait correlations of the 10 species, $a_l = 1 \times 10^{-6} a_p^{-0.504}$ (see Fig. 3).
An increase in phosphorus availability tends to lead to an increase in chlorophyll, but it is also associated with a decrease in light availability due to shading by denser phytoplankton (Edwards et al., 2013a), resulting in a negative correlation between chlorophyll and light. Also, to comprehensively understand this dynamic, it's essential to comprehend the mechanistic process of community structuring. The negative relationship of trait trade-offs is an indicator of mutual exclusivity between the trait trade-offs of interests. To support a deeper understanding let's consider the trophic changes in a lake ecosystem. Fundamentally, variation of the phytoplankton biomass in lake ecosystem is driven by variation in the relative availability of phosphorus and light (Reynolds, 1998; Smith & Nelson, 1986; Sterner & Elser, 2002). An increase in phosphorus availability tends to lead to an increase in chlorophyll, but it is also associated with a decrease in light availability due to shading by denser phytoplankton (Edwards et al., 2013a), resulting in a negative correlation between chlorophyll and light. Also, to comprehensively understand this dynamic, it's essential to consider the trophic changes in a lake ecosystem.
to consider the biology and metabolism of phytoplankton species. The living phytoplankton species acquire resources, including light and nutrients, for their metabolism to produce energy and sustain themselves. Resource competition arises with the seasonal changes in light and varying nutrient content of the water column. The species with high light affinity appear when light is scarce, while those with high nutrient affinity appear when nutrients are scarce. In other words, species can effectively utilize resources when those resources are scarce, a capability that may depend on their specific traits. Thus, resource acquisition trade-offs can be considered the fundamental rule governing population dynamics and community structuring. Hence, identifying potential trade-offs among resources is key to understanding the ecological succession in phytoplankton communities.

Theoretical framework presented in this thesis extends the concepts with new advancements and predictions. This study delves into classical resource competition theory to comprehend the population dynamics of phytoplankton communities. In this theory, within an open system, the most efficient resource competitor benefits from available resources, increases its biomass, and dominates until resource limitations arise due to consumption. Subsequently, lower resource levels can favor other species, prompting an increase in their population. In the context of competition involving two limiting resources, a tradeoff becomes evident, as trait tradeoffs vary among populations. In my research, I explore negative tradeoffs related to resource acquisition traits, specifically the half-saturation constants for light-limited growth and nutrient-limited growth among phytoplankton species. Consequently, changes in light or nutrient availability can benefit different species depending on their resource traits.

4.1 Effects of seasonal varying environmental drivers

Seasonality plays a pivotal role in regulating resource availability throughout the year, impacting community structure. In general, species with a high affinity for light tend to perform relatively better under light-limited conditions, dominating or exhibiting high relative abundance during the spring bloom. Conversely, species with a high nutrient affinity tend to perform relatively better under nutrient-limited conditions, dominating or showing high relative abundance during the peak of summer stratification. Seasonality driven mechanistic processes, including thermal stratification, lead to a nutrient-rich mixed layer during both spring and fall. Specifically, during the fall, the transient abundance of both light and nutrients (Reynolds 2006) contributes to the seasonal variation in phytoplankton blooms. Consequently, these non-limiting conditions regarding the availability of these two resources may favor the dominance of intermediate species. Peeters et al., 2007 provide a detailed explanation of the onset of phytoplankton growth in deep lakes and how meteorology governs turbulent mixing, affecting the phytoplankton bloom. They elucidated that turbulent diffusion is the key factor determining the onset of phytoplankton growth in deep Upper Lake Constance, using a one-dimensional (1-D) mechanistic model combined with a 1-D hydrodynamic model. They showed an excellent agreement between simulation and data, which surprisingly described the thermal stratification of the lake and the onset of phytoplankton growth. According to their investigation, plankton succession depends on the inter-annual variations in mixing dynamics with a complex interplay between heat fluxes, where the mechanisms are governed by meteorological conditions.

They incorporated a new parameter, turbulent diffusion, to represent the physical mechanisms of the vertical thermal profile and profiles of vertical turbulent diffusivities through SIMSTRAT model computation. SIMSTRAT, implemented in FORTRAN, calculated dynamic changes in turbulent kinetic energy ($k$), energy dissipation ($\varepsilon$), and thermal stratification. They
then explained the vertical transport of algae due to turbulent and convective water motions by simulating turbulent diffusivities using the 1-D vertical transport equation Peeters et al. (2007).

Within the scope of this study, I did not treat turbulent diffusivity-governed sinking velocity as a separate variable. However, nutrient regeneration from the sinking process and the losses of algal cells were considered phenomenologically in the model. The model formulation uses sinusoidal functions to represent environmental drivers, providing a simplified description of meteorological conditions. In reality, exceptional temperature effects such as heatwaves and ocean currents, along with changes in the atmosphere and cloud distribution, can alter the regular seasonal patterns. Peeters et al. (2007) confirmed it with their findings suggesting that climate warming and changes in local meteorological conditions are expected to alter the onset of phytoplankton growth, subsequently affecting plankton succession.

In their study of a deep lake, Peeters et al. (2007) found that phytoplankton blooms in Upper Lake Constance are not significantly influenced by variations in photosynthetically active radiation, the sinking velocity of algae, or the effect of water temperature on biological process rates. Instead, these blooms are primarily determined by turbulent diffusion. However, the effects of environmental factors may vary in shallow lakes and marine ecosystems; for instance, shallow lakes, which depend more strongly on the seasonal pattern of solar radiation and water temperature, are much less sensitive to mixing conditions than deep lakes (Peeters et al., 2007). Edward et al. (2012) investigated the effects of temporal environmental variations on the structure of phytoplankton communities, using selected functional traits of phytoplankton taxa within a temperate marine ecosystem. While environmental variables play a significant role in governing physical processes and mechanisms, it's worth noting that biological and geochemical factors are equally crucial for shaping community structure. Edward et al. 2012 highlighted the necessity of considering additional traits that are likely to be important for phytoplankton, including the utilization of Si, P, and Fe, thermal tolerance, and resistance to grazers and viruses within marine or freshwater ecosystems of interest. For instance, the fall bloom, occurring under non-limiting conditions with favorable light and nutrient-rich water, may involve the rapid growth of phytoplankton (Robart et al., 1998). However, strong grazing pressure can significantly affect growth rates. Ehrlich et al. (2020) revealed that defense mechanisms come at the cost of reduced growth rates. As grazing pressure increases seasonally, the community tends to shift towards higher defense levels, sacrificing faster growth rates along the trade-off curve. Importantly, these findings highlight the importance of quantifying trade-offs in understanding the stabilizing mechanisms of community structure, including the fitness of different species, which plays a crucial role in determining community structure. This suggests that assessing trade-offs is essential for predicting community trait adaptation and biodiversity responses to environmental changes.

Moreover, the general patterns of traits and trade-offs can diverge under specific conditions, such as changes in trophic states. In eutrophic conditions, the shading effect caused by the biomass of eutrophic taxa may lead to the dominance of species with higher light affinity and an increase in their relative abundance.

However, it should be noted that the spatial and temporal complexities inherent in these systems can pose challenges to the predictive capacity of analytical frameworks. Thus, while this model captures general seasonal behavior, it may not fully account for variations specific to certain years resulting from natural phenomena or climate change. Nevertheless, this model aids in comprehending and predicting seasonality-driven resource limitations, describing the dynamics of phytoplankton biomass in Lake Constance during its transition from oligotrophic to eutrophic and back to re-oligotrophic conditions. Furthermore, this adaptable framework can
be readily applied to study community structuring in other freshwater or marine phytoplankton ecosystems.

4.2 Other critical model parameters

My primary focus is to comprehend the influence of seasonality on resource acquisition traits and how they impact community structure. To achieve this, I aim to minimize the effects of various critical parameters by maintaining them at constant representative values within the model. This approach enhances our understanding of my primary objective. While many studies have concentrated on the main parameters, some have explored the models with other varying critical parameters. Analyzing this complexity associated with parameters requires a committed numerical analysis supported by validated field experiments. The frequently measured traits include functional traits related to nutrient utilization: maximum cell-specific nutrient uptake rate ($v_{\text{max}}$), the half-saturation constant for nutrient uptake ($K$), and minimum quota ($Q_{\text{min}}$). Functional traits related to light utilization include the predicted growth rate at 10 μmol photons m$^{-2}$s$^{-1}$ ($\mu_{10}$) (Edwards et al., 2013a; Edwards et al., 2013b; Litchman and Klausmeier 2008; Litchman et al., 2004) and maximum specific growth rate ($\mu_{\text{max}}$). Interestingly, they have employed statistical analyses and models that directly correlate the specific maximum growth rates, $\mu_{\text{max}}$ of different phytoplankton species with resource acquisition traits (i.e. nutrient acquisition traits for nitrate, for phosphorous, and light acquisition traits, etc.), considering the influence of environmental gradients (Edwards et al., 2013a; Edwards et al., 2013b).

Peeters et al. (2007) notably incorporated zooplankton grazing into their 1-D mechanistic model using two parameters related to respiration and filtering rates to account for phytoplankton loss. Within their model, phytoplankton biomass was represented by Chl $a$ concentration and utilized a parameter, denoted as $\gamma$, to describe the Chl $a$ to carbon ratio. Additionally, the model considered sinking velocity due to mechanistic effects within the vertical profile.

Moreover, the maximum cellular nutrient concentration $Q_{\text{max}}$, which characterizes a storage capacity (Grover 1991b), is also an important trait in fluctuating nutrient environments. In my study, I have avoided parameterizing specific characteristics, including N-fixation and cellular nutrient quota as I have specifically developed this model to test predefined hypotheses associated with seasonally varying two limiting resources and community structuring. Notably, this numerical model calculates parameters, trends, and future trajectories while reasonably accounting for the average specific growth rate as a constant model parameter.

4.3 Relationship between nutrient supply, $R_{\text{in}}$, and community mean traits

Notably, nutrient enrichment stemming from increased human settlements or intensified industrial activities can lead to abrupt shifts in phytoplankton communities, posing significant risks to human lives and the stability of interconnected ecosystems. Predictability is crucial for understanding these circumstances and implementing appropriate preventive measures to maintain balanced ecosystems in the natural environment.

In the context of my study, I investigated how resource acquisition traits and trade-offs influence the structure of phytoplankton communities under varying light and nutrient conditions. I also examined how community composition changes on an intra-annual basis due to seasonal nutrient fluctuations and increased nutrient enrichment in the lake during eutrophication. It's important to note that several biotic, abiotic, and environmental variables
exist that can impact the lake's community composition. For example, the spring bloom of zooplankton, with a higher grazing rate of filter feeders compared to the production rate of small spring bloom algae, leads to a clear-water phase in June, as described by Sommer in 1984. This process significantly reduces the number of spring bloom algae (known as $r$ strategy). It's important to note that in my study, I did not investigate the effect of grazers as a separate variable. Instead, I incorporated the reduction of biomass resulting from grazing within the loss term of the model. Furthermore, the potential effects of nutrient regeneration by spring bloom zooplankton (by dead cells or excreta) could be explored by incorporating it as a distinct variable, particularly if I introduce a differential function for changes in zooplankton population biomass. In my model, I account for nutrient regeneration resulting from the loss of algal cells due to various factors. This approach facilitates a more comprehensive nutrient mass balance, encompassing the transfer of nutrients across different trophic levels.

Furthermore, variations in summer conditions, such as hydrographic stability, can also exert influence over the composition of the phytoplankton community (Sommer 1985). Dory et al., 2022 investigated the seasonality-driven, climate-change-influenced shifts in phytoplankton assemblages with dissolved organic matter (DOM) properties, utilizing physical and biogeochemical data from sentinel lakes. According to their investigation, the composition of the phytoplankton community varies with DOM.

Phytoplankton communities may employ various coexistence strategies to adapt to their prevailing conditions. For instance, 1) some cyanobacteria enable the acquisition of atmospheric nitrogen, 2) the presence of mixotrophic phytoplankton (heterotrophic and autotrophic modes of nutrition), especially among phytoplankton that are poor competitors for inorganic nutrients, 3) varies in terms of cell size and distribution across nutrient gradients (ex: fast-growing small edible algae dominate the spring bloom, while non-edible larger algae become prevalent in the summer, well-known $r$-strategy and $k$-strategy, respectively), 4) These communities also employ anti-grazer adaptations through various physiological developments, including changes in overall size, morphology, extracellular mucilage production, and maintenance of high C:nutrient ratios (Reynolds 2006, Sterner 1989) and some species even produce toxins that deter grazers (Anderson et al., 1998, Huisman et al., 2005).

To avoid the complications that can arise with regard to the species within the phytoplankton community, given their diversity in resource acquisition, morphological variation, natural enemy interactions, responses to environmental changes (e.g., hydrographical stability), and modes of reproduction, the analysis of community mean traits emerges as a suitable and rational approach to decipher how a community collectively responds to specific traits. The empirical data related to resource acquisition traits provided me with insights to adapt representative trait values for parameterizing the developed model. I could then compute reasonable CMT $\alpha$ and $\alpha_P$ values to derive the expected trade-offs for varying inter-annual and intra-annual variations of nutrients.

4.4 Conclusions
In conclusion, the observed general patterns of seasonal dominance among various phytoplankton species in model simulations, coupled with the predicted differences in relative species abundance across diverse nutrient supply levels, are in accordance with trends indicative of resource limitation. These findings align consistently with empirical observations. The trait-based approach investigated in this study significantly contributes to elucidating the mechanisms governing the coexistence of phytoplankton species in response to trophic state changes.
Acknowledgement

I would like to express my deepest gratitude to my supervisor, Professor Sebastian Diehl, whose unwavering support and expert guidance made this work possible. His mentorship carried me through every stage of this project, providing me with invaluable opportunities to learn and acquire skills in the mathematical modeling of ecosystem dynamics. His experience, knowledge, and commitment to high standards have undoubtedly made me better at what I do. I am also thankful to Associate Professor Tom Korsman for his continuous guidance and assistance, which greatly contributed to the success of this project. My sincere appreciation goes to my family for their unwavering support during the completion of this project, especially amidst the stress and challenges associated with relocation. Throughout my academic career, we have lived in three countries across two continents, and I completed this work during our relocation to yet another country. The courage and unity exhibited by my family were a blessing on this journey.

Finally, I extend my gratitude to Umeå University for providing me with this opportunity. I must also acknowledge the significance of the free education system in Sri Lanka, from school to university, which allowed me to receive an education as a person from an underrepresented community. Without this support, I would not have had the opportunity to study at Umeå University and my previous institution, Saitama University in Japan as a MEXT scholar. This experience reminds me of the weight of the responsibility I carry and motivates me to contribute meaningfully to make a positive impact.

5. References


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Appendix 1

Appendix Figure 1. Seasonal trajectories of the biomasses of phytoplankton species A1-A10 (upper row of panels), the total light attenuation coefficient (i.e., the sum of background light attenuation plus attenuation by phytoplankton biomass = $k_{bg} + k \sum_{i=1}^{10} A_i$) (middle row of panels), and the concentration of mineral phosphorus in the water column (bottom row of panels). Examples of low (= 6 mg P/m$^3$, column a), intermediate (= 50 mg P/m$^3$, column b) and high (= 100 mg P/m$^3$, column c) nutrient supply are shown in a 5-year simulation, with consistent seasonal trajectories. The x-axes are scaled in units of day of the year.
Appendix Figure 2. Seasonal trajectories of changes of relative contribution to the total biomass of phytoplankton species A1-A10 for example simulation of (= 6, 10, 30, 50, 80, and 100 mg P/m$^3$, a-f) nutrient supply. The x-axes are scaled in units of day of the year.
Appendix 2

Appendix Two includes the developed model with a simulation of ten phytoplankton species (MATLAB code 1) and the inter-annual community dynamics for varying $R_{in}$ concentrations due to nutrient loading, simulating eutrophication and re-oligotrophication of Lake Constance. Other codes for the simulation of environmental variables and figures will be available upon request.

MATLAB code 1: Model simulations of ten phytoplankton species exposed to varying environmental conditions.

```matlab
clc
clear all
close all

% Define parameters
Ia = 330; % Vertical shift (seasonal changes in incident light In)
Ib = -250; % Amplitude
Ic = 4.51; % Horizontal shift.
Da = 0.3015; % Vertical shift (seasonal changes in mixing D)
Db = -0.2915; % Amplitude
Dc = 0.55*pi; % Horizontal shift
Dd = 62.5; % Percentage of the year with low mixing (stratification period)
Ta = 15; % Vertical shift (seasonal changes in temperature)
Tb = -10; % Amplitude
Tc = 5.4; % Horizontal shift
k  = 0.0003; % specific light attenuation coefficient of algal biomass
Kbg = 0.25; % background light attenuation coefficient
z = 20; % depth of the water column
M1 = 0.45; % half-saturation constant for P-limited production of A1
M2 = 0.25; % half-saturation constant for P-limited production of A2
M3 = 0.14; % half-saturation constant for P-limited production of A3
M4 = 0.08; % half-saturation constant for P-limited production of A4
M5 = 0.045; % half-saturation constant for P-limited production of A5
M6 = 0.025; % half-saturation constant for P-limited production of A6
M7 = 0.014; % half-saturation constant for P-limited production of A7
M8 = 0.008; % half-saturation constant for P-limited production of A8
M9 = 0.0045; % half-saturation constant for P-limited production of A9
M10 = 0.0025; % half-saturation constant for P-limited production of A10
H1 = 20.93*M1^(-0.504); % fitted half-saturation constant for light-limited production of A1
H2 = 20.93*M2^(-0.504); % fitted half-saturation constant for light-limited production of A2
H3 = 20.93*M3^(-0.504); % fitted half-saturation constant for light-limited production of A3
H4 = 20.93*M4^(-0.504); % fitted half-saturation constant for light-limited production of A4
H5 = 20.93*M5^(-0.504); % fitted half-saturation constant for light-limited production of A5
H6 = 20.93*M6^(-0.504); % fitted half-saturation constant for light-limited production of A6
```
H7 = 20.93*M7^(-0.504); \% fitted half-saturation constant for light-limited production of A7
H8 = 20.93*M8^(-0.504); \% fitted half-saturation constant for light-limited production of A8
H9 = 20.93*M9^(-0.504); \% fitted half-saturation constant for light-limited production of A9
H10 = 20.93*M10^(-0.504); \% fitted half-saturation constant for light-limited production of A10

q = 0.02; \% nutrient content per unit algal biomass (g P/g C)
a = 0.1; \% coefficient of temperature dependence of algal growth
P0 = 0.2; \% reference maximum specific production rate of all species at 0 degrees Celsius
l0 = 0.013; \% reference background loss rate at 0 degrees Celsius
f = 0.5; \% fraction of recycled nutrients from algal background losses
Im = 0.1; \% Immigration rate from resting stages
Rin = 100; \% concentration of nutrient in deep water

% Run the model from initial condition (R0, A0) and plot the results

% Set options for ODE-solver
ode_opts = odeset('reltol', 1e-6 , 'abstol', 1e-6);

% Put initial conditions into initial vector S0
S0 = [ A10; A20; A30; A40; A50; A60; A70; A80; A90; A100; AT0; R0 ;RT0];

% Use the solver ode45 to solve the seasonality model:
[t,S] = ode15s(@(t,S)seasonality_model(t,S,Ia,Ib,Ic,Da,Db,Dc,Dd,Ta,Tb,Tc,Rin,M1,M2,M3,M4,M5,M6,M7,M8,M9,M10,q,k,Kbg,z,H1,H2,H3,H4,H5,H6,H7,H8,H9,H10,a,P0,Im,l0,f) , [t_0:1:t_end] , S0, ode_opts );

% % Plot solutions
figure (1)
subplot(3,1,1);
hold on;
%ylim ([0 2])
%xlim ([0 50])
plot( t, S(:,1), '-g' )
plot( t, S(:,2), '-b' )
plot( t, S(:,3), '-k' )
plot( t, S(:,4), '-r' )
plot( t, S(:,5), '-m' )
plot( t, S(:,6), '--m' )
plot( t, S(:,7), '--r' )
plot( t, S(:,8), '--b' )
plot( t, S(:,9), '--b' )
plot( t, S(:,10), '--g' )
legend('A1', 'A2', 'A3', 'A4', 'A5', 'A6', 'A7', 'A8', 'A9', 'A10')
ylabel({'Algal biomass'; '(mg C/m^3)'});
%xlabel('Time (Days)')
xlim ([0 2000])
ylim ([0 2500])
hold off;

% subplot(3,1,2); % use this code if you want to plot total biomass
% %ylim ([0 2])
% %xlim ([0 50])
% plot( t, S(:,11), '-k')
% legend('Total algal biomass')
ylabel('Algal biomass (mg C/m^3)');
% xlabel('Time (Days)')
xlim ([0 2000])
ylim ([0 4000])

%% I use the light attenuation plot instead of total biomass
% Kd plot
% Create a vector to store the calculated specific light attenuation coefficient of total biomass
total_biomass_light_attenuation_vec = ((k*S(:,11))+Kbg).*ones(1826,1);
subplot(3,1,2);
plot(total_biomass_light_attenuation_vec)
xlim ([0 2000])
ylim ([0.2 1.4])
ylabel({'Specific light attenuation'; 'coefficient [m^2/mg C]'})
xlabel('Time (Days)', 'FontSize',14)
legend('Total light attenuation')

subplot(3,1,3); % Plot dissolved nutrient
hold on;
plot( t, S(:,12), '-r' )
% plot( t, S(:,13), '-b' ) % 'Total nutrient'
legend('Dissolved nutrient')
ylabel({'Nutrient concentration';'(mg P/m^3)'}))
xlabel('Time (Days)')
xlim ([0 2000])
ylim ([0 100])

%total biomass last year
figure
subplot(2,1,2); % hold on;
tot_biomass_last_year = zeros(365,1);

% Calculate the biomass from each species to calculate total biomass of a % year (consider each day)

% looping over each species
for i=1:10
    tot_biomass_last_year = tot_biomass_last_year + S(end-364:end,i);
end
plot(tot_biomass_last_year)
% Calculate yearly average (average of the each day through the year)

    total_biomass_yearly_average = sum(tot_biomass_last_year)/365;

% Create a vector to store the calculated average values

    total_biomass_yearly_average_vec = total_biomass_yearly_average.*ones(365,1);

    plot(total_biomass_yearly_average_vec)
    xlim ([0 365])
    ylim ([0 3500])
    ylabel({'Total biomass';'
             [mg C/m^3]'})
    xlabel('Time (Days)')
    legend('Total biomass', 'Yearly average')

    hold off

% contribution of each species to total biomass
% figure

    contrib_s1 = S(end-364:end,1)./tot_biomass_last_year;
    contrib_s2 = S(end-364:end,2)./tot_biomass_last_year;
    contrib_s3 = S(end-364:end,3)./tot_biomass_last_year;
    contrib_s4 = S(end-364:end,4)./tot_biomass_last_year;
    contrib_s5 = S(end-364:end,5)./tot_biomass_last_year;
    contrib_s6 = S(end-364:end,6)./tot_biomass_last_year;
    contrib_s7 = S(end-364:end,7)./tot_biomass_last_year;
    contrib_s8 = S(end-364:end,8)./tot_biomass_last_year;
    contrib_s9 = S(end-364:end,9)./tot_biomass_last_year;
    contrib_s10 = S(end-364:end,10)./tot_biomass_last_year;

    subplot(2,1,1);
    hold on;
    plot(contrib_s1, '-g')
    plot(contrib_s2, '-b')
    plot(contrib_s3, '-k')
    plot(contrib_s4, '-r')
    plot(contrib_s5, '-m')
    plot(contrib_s6, '--m')
    plot(contrib_s7, '--r')
    plot(contrib_s8, '--k')
    plot(contrib_s9, '--b')
    plot(contrib_s10, '--g')
    legend('A1', 'A2', 'A3', 'A4', 'A5', 'A6', 'A7', 'A8', 'A9', 'A10')
    ylabel({'Relative contribution';'
            to the tot.biomass'})
    % xlabel('Time (Days)')
    xlim ([0 365])
mean_contribution_species_1 = mean(contrib_s1);
mean_contribution_species_2 = mean(contrib_s2);
mean_contribution_species_3 = mean(contrib_s3);
mean_contribution_species_4 = mean(contrib_s4);
mean_contribution_species_5 = mean(contrib_s5);
mean_contribution_species_6 = mean(contrib_s6);
mean_contribution_species_7 = mean(contrib_s7);
mean_contribution_species_8 = mean(contrib_s8);
mean_contribution_species_9 = mean(contrib_s9);
mean_contribution_species_10 = mean(contrib_s10);

% Calculation of mean community phosphate and light affinities (CMT_gamma, CMT_alpha)
% These calculations involve Pmax at T = 20 degrees C, i.e. P0*exp(a*20),
% and in the case of light affinity a division by the number of seconds per
% day (86400):
CMT_gamma = P0*exp(a*20) * exp( log(1/M1)*mean(contrib_s1) +
log(1/M2)*mean(contrib_s2) + log(1/M3)*mean(contrib_s3) + log(1/M4)*mean(contrib_s4) +
log(1/M5)*mean(contrib_s5) + log(1/M6)*mean(contrib_s6) +...
\[ \log\left(\frac{1}{M_7}\right) \times \text{mean}(\text{contrib}_{s7}) + \log\left(\frac{1}{M_8}\right) \times \text{mean}(\text{contrib}_{s8}) + \log\left(\frac{1}{M_9}\right) \times \text{mean}(\text{contrib}_{s9}) + \log\left(\frac{1}{M_{10}}\right) \times \text{mean}(\text{contrib}_{s10}) \]

\[ CMT_{\alpha} = P_0 \times e^{a \times 20}/86400 \times \exp\left( \log\left(\frac{1}{H_1}\right) \times \text{mean}(\text{contrib}_{s1}) + \log\left(\frac{1}{H_2}\right) \times \text{mean}(\text{contrib}_{s2}) + \log\left(\frac{1}{H_3}\right) \times \text{mean}(\text{contrib}_{s3}) + \log\left(\frac{1}{H_4}\right) \times \text{mean}(\text{contrib}_{s4}) + \log\left(\frac{1}{H_5}\right) \times \text{mean}(\text{contrib}_{s5}) + \log\left(\frac{1}{H_6}\right) \times \text{mean}(\text{contrib}_{s6}) + \log\left(\frac{1}{H_7}\right) \times \text{mean}(\text{contrib}_{s7}) + \log\left(\frac{1}{H_8}\right) \times \text{mean}(\text{contrib}_{s8}) + \log\left(\frac{1}{H_9}\right) \times \text{mean}(\text{contrib}_{s9}) + \log\left(\frac{1}{H_{10}}\right) \times \text{mean}(\text{contrib}_{s10}) \right) \]

\% Kd plot
\% Create a vector to store the calculated specific light attenuation coefficient of total biomass
\text{total\_biomass\_light\_attenuation\_vec} = ((k \times S(:,11))+Kbg) \times \text{ones}(1826,1);

\% Here I plot the total light attenuation for 5 years of time steps
\text{figure}
\text{plot (total\_biomass\_light\_attenuation\_vec)}
\text{xlim ([0 1826])}
\text{ylim ([0.2 1.4])}
\text{ylabel('Specific light attenuation coefficient [m^2/mg C]')} \% m2/mg C
\text{xlabel('Time (Days)')} \% m2/mg C
\text{legend('Total light attenuation')}
% This plot will be in the results section, for this plot only last years changes will be considered

% hold on;
% algal_biomass_last_year = zeros(365,1);

% Algal biomass
%%% Empty vectors to store the algal biomass data
A1_biomass_last_year = zeros(365,1);
A2_biomass_last_year = zeros(365,1);
A3_biomass_last_year = zeros(365,1);
A4_biomass_last_year = zeros(365,1);
A5_biomass_last_year = zeros(365,1);
A6_biomass_last_year = zeros(365,1);
A7_biomass_last_year = zeros(365,1);
A8_biomass_last_year = zeros(365,1);
A9_biomass_last_year = zeros(365,1);
A10_biomass_last_year = zeros(365,1);

% Calculate the biomass from each species biomass of a year (consider each day)
A1_biomass_last_year = A1_biomass_last_year + S(end-364:end,1);
A2_biomass_last_year = A2_biomass_last_year + S(end-364:end,2);
A3_biomass_last_year = A3_biomass_last_year + S(end-364:end,3);
A4_biomass_last_year = A4_biomass_last_year + S(end-364:end,4);
A5_biomass_last_year = A5_biomass_last_year + S(end-364:end,5);
A6_biomass_last_year = A6_biomass_last_year + S(end-364:end,6);
A7_biomass_last_year = A7_biomass_last_year + S(end-364:end,7);
A8_biomass_last_year = A8_biomass_last_year + S(end-364:end,8);
A9_biomass_last_year = A9_biomass_last_year + S(end-364:end,9);
A10_biomass_last_year = A10_biomass_last_year + S(end-364:end,10);

figure
subplot(3,1,1); % Algal biomass last year plot
hold on
plot( A1_biomass_last_year, '-g' )
plot( A2_biomass_last_year, '-b' )
plot(A3_biomass_last_year, '-k' )
plot(A4_biomass_last_year, '-r' )
plot(A5_biomass_last_year, '-m' )
plot(A6_biomass_last_year, '--m' )
plot(A7_biomass_last_year, '--r' )
plot(A8_biomass_last_year, '--k' )
plot(A9_biomass_last_year, '--b' )
plot(A10_biomass_last_year, '--g' )
legend('A1','A2','A3','A4','A5','A6','A7','A8','A9','A10')
ylabel({'Algal biomass'; '(mg C/m^3)'});
xlim ([0 400])
ylim ([0 2500])
% title('Total biomass')
hold off

% Light attenuation
total_biomass_light_attenuation_vec = ((k*S(:,11))+Kbg).*ones(1826,1);
% Kd plot
% Create a vector to store the calculated specific light attenuation coefficient of total biomass
total_biomass_light_attenuation_last_year = zeros(365,1);
total_biomass_light_attenuation_last_year = total_biomass_light_attenuation_last_year +
total_biomass_light_attenuation_vec(end-364:end,1);

subplot(3,1,2); % Light attenuation plot
% plot (t(end-364:end), total_biomass_light_attenuation_vec(end-364:end))
plot (total_biomass_light_attenuation_last_year);
xlim ([0 400])
ylim ([0.2 1.4])
ylabel({'Specific light attenuation'; 'coefficient [m^2/mg C]'})% m2/mg C
%xlabel('Time (Days)')
legend('Total light attenuation')

% Dissolve nutrient
%%% Empty vectors to store the dissolve nutrient data
dissolved_nutrients_last_year = zeros(365,1);
dissolved_nutrients_last_year = dissolved_nutrients_last_year + S(end-364:end,12);

subplot(3,1,3);
hold on;
plot( dissolved_nutrients_last_year, '-r' )
% plot( t, S(:,13), '-b' ) % 'Total nutrient'
legend('Dissolved nutrient')
ylabel({'Nutrient concentration'; '(mg P/m^3)'})
xlabel('Time (Days)')
xlim ([0 400])
ylim ([0 100])
%set(findall(gcf,'-property','FontSize'),'FontSize',14)
hold off;
function dSdt = seasonality_model(t,S,Ia,Ib,Ic,Da,Db,Dd,Ta,Tc,Rin,M1,M2,M3,M4,M5,M6,M7,M8, M9,M10,q,k,Kbg,z,H1,H2,H3,H4,H5,H6,H7,H8,H9,H10,a,P0,l0,f)

% Get the first 7 elements of S, and name them A1, A2, A3, A4, A5, AT, R, and RT
A1 = S(1);
A2 = S(2);
A3 = S(3);
A4 = S(4);
A5 = S(5);
A6 = S(6);
A7 = S(7);
A8 = S(8);
A9 = S(9);
A10 = S(10);
AT = S(11);
R  = S(12);
RT = S(13);

% Seasonal change in exchange rate D with deep water
% D = Da+Db*sin(0.0172*t-Dc);
% (this expression is used when D follows a sine wave)
D = Da+Db*(0.8*square(2*pi/365*t-Dc, Dd)+0.2*sin(2*pi/365*t-Dc-0.6));
% (this expression is used when D follows the sum of a square wave and a sine wave)
% Seasonal change of temperature
T = Ta + Tb * sin(0.0172 * t - Tc); 2 * pi / 365 = 0.0172 defines the periodicity
% Temperature dependence of pmax
Pmax = P0 * exp(a * T); temp dependence of Pmax of all species
% Temperature dependence of background loss rate
l = l0 * exp(a * T); temp dependence of l of all species
% Seasonal change in light
Iin = Ia + Ib * sin(0.0172 * t - Ic); 2 * pi / 365 = 0.0172 defines the periodicity
% Calculate total light extinction coefficient
Kd = k * (A1 + A2 + A3 + A4 + A5 + A6 + A7 + A8 + A9 + A10) + Kbg;
% Calculate Iout
Iout = Iin * exp(-Kd * z);

% The nutrient uptake by each species were subdivided for the convenience
dRdt_A1 = q * (Pmax / Kd * log((H1 + Iin) / (H1 + Iout)) * R / (M1 + R)) * A1 / z;
dRdt_A2 = q * (Pmax / Kd * log((H2 + Iin) / (H2 + Iout)) * R / (M2 + R)) * A2 / z;
dRdt_A3 = q * (Pmax / Kd * log((H3 + Iin) / (H3 + Iout)) * R / (M3 + R)) * A3 / z;
dRdt_A4 = q * (Pmax / Kd * log((H4 + Iin) / (H4 + Iout)) * R / (M4 + R)) * A4 / z;
dRdt_A5 = q * (Pmax / Kd * log((H5 + Iin) / (H5 + Iout)) * R / (M5 + R)) * A5 / z;
dRdt_A6 = q * (Pmax / Kd * log((H6 + Iin) / (H6 + Iout)) * R / (M6 + R)) * A6 / z;
dRdt_A7 = q * (Pmax / Kd * log((H7 + Iin) / (H7 + Iout)) * R / (M7 + R)) * A7 / z;
dRdt_A8 = q * (Pmax / Kd * log((H8 + Iin) / (H8 + Iout)) * R / (M8 + R)) * A8 / z;
dRdt_A9 = q * (Pmax / Kd * log((H9 + Iin) / (H9 + Iout)) * R / (M9 + R)) * A9 / z;
dRdt_A10 = q * (Pmax / Kd * log((H10 + Iin) / (H10 + Iout)) * R / (M10 + R)) * A10 / z;

% Compute dR/dt
dRdt = D * (Rin - R) + q * f * l * (A1 + A2 + A3 + A4 + A5 + A6 + A7 + A8 + A9 + A10) - dRdt_A1 - dRdt_A2 - dRdt_A3 - dRdt_A4 - dRdt_A5 - dRdt_A6 - dRdt_A7 - dRdt_A8 - dRdt_A9 - dRdt_A10;

% Compute Ai/dt
dA1dt = Im + Pmax / Kd * log((H1 + Iin) / (H1 + Iout)) * R / (M1 + R) * A1 / z - (D + l) * A1;
dA2dt = Im + Pmax / Kd * log((H2 + Iin) / (H2 + Iout)) * R / (M2 + R) * A2 / z - (D + l) * A2;
dA3dt = Im + Pmax / Kd * log((H3 + Iin) / (H3 + Iout)) * R / (M3 + R) * A3 / z - (D + l) * A3;
dA4dt = Im + Pmax / Kd * log((H4 + Iin) / (H4 + Iout)) * R / (M4 + R) * A4 / z - (D + l) * A4;
dA5dt = Im + Pmax / Kd * log((H5 + Iin) / (H5 + Iout)) * R / (M5 + R) * A5 / z - (D + l) * A5;
dA6dt = Im + Pmax / Kd * log((H6 + Iin) / (H6 + Iout)) * R / (M6 + R) * A6 / z - (D + l) * A6;
dA7dt = Im + Pmax / Kd * log((H7 + Iin) / (H7 + Iout)) * R / (M7 + R) * A7 / z - (D + l) * A7;
dA8dt = Im + Pmax / Kd * log((H8 + Iin) / (H8 + Iout)) * R / (M8 + R) * A8 / z - (D + l) * A8;
dA9dt = Im + Pmax / Kd * log((H9 + Iin) / (H9 + Iout)) * R / (M9 + R) * A9 / z - (D + l) * A9;
dA10dt = Im + Pmax / Kd * log((H10 + Iin) / (H10 + Iout)) * R / (M10 + R) * A10 / z - (D + l) * A10;

% Compute total algal biomass
dATdt = dA1dt + dA2dt + dA3dt + dA4dt + dA5dt + dA6dt + dA7dt + dA8dt + dA9dt + dA10dt;

% Compute total nutrient concentration
dRTdt = q * dATdt + dRdt;
% Put dR/dt, dA1/dt, dA2/dt, dA3/dt, dA4/dt, dA5/dt and dAT/dt into the column vector dS/dt

\[
\]

end
MATLAB code 2: Inter-annual community dynamics for varying $R_{in}$ concentration due to nutrient loading [simulated eutrophication and re-oligotrophication]

clc
clear all
close all

% Define parameters
Ia = 330; % Vertical shift (seasonal changes in incident light In)
Ib = -250; % Amplitude
Ic = 4.51; % Horizontal shift.
Da = 0.3015; % Vertical shift (seasonal changes in mixing D)
Db = -0.2915; % Amplitude
Dc = 0.55*pi; % Horizontal shift
Dd = 62.5; % Percentage of the year with low mixing (stratification period)
Ra = 45; % Vertical shift (Ra + Rb gives minimum and Ra - Rb gives maximum of sine curve)
Rb = -40; % Amplitude
Rc = 3*pi/2; % Horizontal shift
Ta = 15; % Vertical shift (seasonal changes in temperature)
Tb = -10; % Amplitude
Tc = 5.4; % Horizontal shift
k = 0.0003; % specific light attenuation coefficient of algal biomass
Kbg = 0.25; % background light attenuation coefficient
z = 20; % depth of the water column
M1 = 0.45; % half-saturation constant for P-limited production of A1
M2 = 0.25; % half-saturation constant for P-limited production of A2
M3 = 0.14; % half-saturation constant for P-limited production of A3
M4 = 0.08; % half-saturation constant for P-limited production of A4
M5 = 0.045; % half-saturation constant for P-limited production of A5
M6 = 0.025; % half-saturation constant for P-limited production of A6
M7 = 0.014; % half-saturation constant for P-limited production of A7
M8 = 0.008; % half-saturation constant for P-limited production of A8
M9 = 0.0045; % half-saturation constant for P-limited production of A9
M10 = 0.0025; % half-saturation constant for P-limited production of A10
H1 = 20.93*M1^(-0.504); % fitted half-saturation constant for light-limited production of A1
H2 = 20.93*M2^(-0.504); % fitted half-saturation constant for light-limited production of A2
H3 = 20.93*M3^(-0.504); % fitted half-saturation constant for light-limited production of A3
H4 = 20.93*M4^(-0.504); % fitted half-saturation constant for light-limited production of A4
H5 = 20.93*M5^(-0.504); % fitted half-saturation constant for light-limited production of A5
H6 = 20.93*M6^(-0.504); % fitted half-saturation constant for light-limited production of A6
H7 = 20.93*M7^(-0.504); % fitted half-saturation constant for light-limited production of A7
H8 = 20.93*M8^(-0.504); % fitted half-saturation constant for light-limited production of A8
H9 = 20.93*M9^(-0.504); % fitted half-saturation constant for light-limited production of A9
H10 = 20.93*M10^(-0.504); % fitted half-saturation constant for light-limited production of A10
q = 0.02; % nutrient content per unit algal biomass (g P/g C)
a = 0.1; % coefficient of temperature dependence of algal growth
P0 = 0.2; % reference maximum specific production rate of all species at 0 degrees Celsius
l = 0.1; % background loss rate of algae
l0 = 0.013; % reference background loss rate at 0 degrees Celsius
f = 0.5; % fraction of recycled nutrients from algal background losses
Im = 0.1; % Immigration rate from resting stages
Rin = 195; % concentration of nutrient in deep water
% Run the model from initial condition (R0, A0) and plot the results
% t_0 = 0; % start time
% t_end = 60*365; % end time
A10 = 10; % initial algal biomass of A1
A20 = 10; % initial algal biomass of A2
A30 = 10; % initial algal biomass of A3
A40 = 10; % initial algal biomass of A4
A50 = 10; % initial algal biomass of A5
A60 = 10; % initial algal biomass of A6
A70 = 10; % initial algal biomass of A7
A80 = 10; % initial algal biomass of A8
A90 = 10; % initial algal biomass of A9
A100 = 10; % initial algal biomass of A10
Rin0 = 1;
AT0 = A10+A20+A30+A40+A50+A60+A70+A80+A90+A100; % initial total algal biomass AT
R0 = Rin0; % initial nutrient concentration (mg P/m3)
RT0 = q*AT0+R0; % initial total nutrient concentration
% Rin = Ra+Rb*sin(0.0002869*t-Rc);

% Set options for ODE-solver
ode_opts = odeset( 'reltol' , 1e-6 , 'abstol' , 1e-6 );
% Put initial conditions into initial vector S0
S0 = [ A10; A20; A30; A40; A50; A60; A70; A80; A90; A100; AT0; R0 ;RT0];

% Define the vector of r values that will be used to generate the bifurcation plot:
Rin_iter = 60; % Choose how many different Rin values will be investigated for population minima and maxima. Different Rin value for each year
% Define the range of r-values
Rin_range = linspace( 5 , 85 , Rin_iter )';

% Create vectors that will store the min and max values from a given late time span of the simulations
S_eq_min = zeros( Rin_iter , 85 );
S_eq_max = zeros( Rin_iter , 85 );
% Loop over all r-values
for RinRin = 1 : length( Rin_range )
    % Set r to first and all subsequent values in the vector r_range
    Rin = Rin_range(RinRin);
    % Solve the ODE system:
    % Use the solver ode45 to solve the seasonality model:
    [t,S] = ode15s(@(t,S)seasonality_model(t,S,Ia,Ib,Ic,Da,Db,Dc,Dd,Ra,Rb,Rc, Ta,Tc,M1,M2,M3,M4,M5, M6,M7,M8,M9,M10,q,k,Kbg,z,H1,H2,H3,H4,H5,H6,H7,H8,H9,H10,a,P0,Im,l0,f),
    [t_0:1:t_end] , S0, ode_opts );
end

figure
subplot(2,1,1);
hold on;
%ylim ([0 2])
%xlim ([0 50])
plot( t, S(:,1), '-g' )
plot( t, S(:,2), '-b' )
plot( t, S(:,3), '-k' )
plot( t, S(:,4), '-r' )
plot( t, S(:,5), '-m' )
plot( t, S(:,6), '--m' )
plot( t, S(:,7), '--r' )
plot( t, S(:,8), '--k' )
plot( t, S(:,9), '--b' )
plot( t, S(:,10), '--g' )
legend('A1', 'A2', 'A3', 'A4', 'A5', 'A6', 'A7', 'A8', 'A9', 'A10')
ylabel('Algal biomass (mg C/m^3)')
xlabel('Time (Days)')
xlim([0 21900])
xticks(0:3650:365*60)
% ylim ([0 5000])
hold off;
subplot(2,1,2);
%ylim ([0 2])
%xlim ([0 50])
% plot( t, S(:,11), '-k' ) % This is for the "Total algal biomass" instead I
% am going to use "dissolved P" so I will comment this for a moment
% legend('Total algal biomass')
% ylabel('Algal biomass (mg C/m^3)')
plot( t, S(:,12), '-k')
legend('Dissolved phosphorous')
ylabel({'Phosphorus concentration';'(mg P/m^3)'})
% Primary x-axis
xlabel('Time (Days)')
xlim([0 21900])
xticks(0:3650:365*60)
% Secondary x-axis
% Change the y-axis color to black
ax = gca; % axis define as gca 'get current axis' this is to handle the current axis
ax.YColor = 'k';

% Create secondary x-axis for years
yyaxis right % the y-axis in the right
ax2 = gca;
set(ax2, 'Color', 'none', 'YTick', [], 'YTickLabel', [], 'YColor', 'k');
ax2_pos = ax2.Position;

% Adjust the position to create a gap between primary and secondary x-axes
ax2_line = axes('Position', [ax2_pos(1), ax2_pos(2)-0.065, ax2_pos(3), ax2_pos(4)], 'Color', 'none', 'YTick', [], 'XTick', 0:3650:365*60, 'XTickLabel', 1950:10:2010, 'XColor', 'k');
xlabel('Year');
xlim(ax2_line, [0 21900]);

figure
plot( t, S(:,12), '-k')
legend('Dissolved nutrient')
ylabel({'Nutrient concentration';'(mg P/m^3)'}))

% Primary x-axis
xlabel('Time (Days)')
xlim([0 21900])
xticks(0:3650:365*60)
function dSdt =
seasonality_model(t,S,Ia,Ib,Ic,Db,Dc,Dd,Ra,Rb,Rc,Ta,Tb,Tc,M1,M2,M3,M4,M5,M6,M7
,M8,M9,M10,q,k,Kbg,z,H1,H2,H3,H4,H5,H6,H7,H8,H9,H10,a,P0,Im,l0,f)
% Get the first 7 elements of S, and name them A1, A2, A3, A4, A5, AT, R, and RT
A1 = S(1);
A2 = S(2);
A3 = S(3);
A4 = S(4);
A5 = S(5);
A6 = S(6);
A7 = S(7);
A8 = S(8);
A9 = S(9);
A10 = S(10);
AT = S(11);
R = S(12);
RT = S(13);

% Seasonal change in exchange rate D with deep water
% D = Da+Db*sin(0.0172*t-Dc);
% (this expression is used when D follows a sine wave)
D = Da+Db*(0.8*square(2*pi/365*t-Dc, Dd)+0.2*sin(2*pi/365*t-Dc-0.6));
% (this expression is used when D follows the sum of a square wave and a sine wave)
% Seasonal change of Rin
\[ R_{in} = R_a + R_b \sin(0.0002869 \cdot t - R_c); \] % \( \frac{2\pi}{(60 \cdot 365)} = 0.0002869 \) defines the periodicity (60 years)

% Seasonal change of temperature
\[ T = T_a + T_b \sin(0.0172 \cdot t - T_c); \]

% Temperature dependence of \( P_{max} \)
\[ P_{max} = P_0 \exp(a \cdot T); \] % Temperature dependence of \( P_{max} \) of all species

% Temperature dependence of background loss rate
\[ l = l_0 \exp(a \cdot T); \] % Temp dependence of \( l \) of all species

% Seasonal change in light
\[ I_{in} = I_a + I_b \sin(0.0172 \cdot t - I_c); \]

% Calculate total light extinction coefficient
\[ K_d = k(A_1 + A_2 + A_3 + A_4 + A_5 + A_6 + A_7 + A_8 + A_9 + A_{10}) + K_{bg}; \]

% Calculate \( I_{out} \)
\[ I_{out} = I_{in} \exp(-K_d \cdot z); \]

% The nutrient uptake by each species were subdivided for the convenience
\[
\begin{align*}
\frac{dR}{dt}_{A_1} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_1 + I_{in}}{H_1 + I_{out}} \right) \frac{R}{M_1 + R} \right) \frac{A_1}{z} \\
\frac{dR}{dt}_{A_2} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_2 + I_{in}}{H_2 + I_{out}} \right) \frac{R}{M_2 + R} \right) \frac{A_2}{z} \\
\frac{dR}{dt}_{A_3} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_3 + I_{in}}{H_3 + I_{out}} \right) \frac{R}{M_3 + R} \right) \frac{A_3}{z} \\
\frac{dR}{dt}_{A_4} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_4 + I_{in}}{H_4 + I_{out}} \right) \frac{R}{M_4 + R} \right) \frac{A_4}{z} \\
\frac{dR}{dt}_{A_5} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_5 + I_{in}}{H_5 + I_{out}} \right) \frac{R}{M_5 + R} \right) \frac{A_5}{z} \\
\frac{dR}{dt}_{A_6} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_6 + I_{in}}{H_6 + I_{out}} \right) \frac{R}{M_6 + R} \right) \frac{A_6}{z} \\
\frac{dR}{dt}_{A_7} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_7 + I_{in}}{H_7 + I_{out}} \right) \frac{R}{M_7 + R} \right) \frac{A_7}{z} \\
\frac{dR}{dt}_{A_8} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_8 + I_{in}}{H_8 + I_{out}} \right) \frac{R}{M_8 + R} \right) \frac{A_8}{z} \\
\frac{dR}{dt}_{A_9} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_9 + I_{in}}{H_9 + I_{out}} \right) \frac{R}{M_9 + R} \right) \frac{A_9}{z} \\
\frac{dR}{dt}_{A_{10}} &= q \left( \frac{P_{max}}{K_d} \log \left( \frac{H_{10} + I_{in}}{H_{10} + I_{out}} \right) \frac{R}{M_{10} + R} \right) \frac{A_{10}}{z} \\
\end{align*}
\]

% Compute \( dR/dt \)
\[
\begin{align*}
\frac{dR}{dt} &= D \left( R_{in} - R \right) + q f l (A_1 + A_2 + A_3 + A_4 + A_5 + A_6 + A_7 + A_8 + A_9 + A_{10}) \\
&\quad - \frac{dR}{dt}_{A_1} - \frac{dR}{dt}_{A_2} - \frac{dR}{dt}_{A_3} - \frac{dR}{dt}_{A_4} - \frac{dR}{dt}_{A_5} - \frac{dR}{dt}_{A_6} - \frac{dR}{dt}_{A_7} - \frac{dR}{dt}_{A_8} - \frac{dR}{dt}_{A_9} - \frac{dR}{dt}_{A_{10}};
\end{align*}
\]

% Now our \( R_{in} \) also change with the time. Previously, we assumed that we have a constant \( R_{in} \)
\[
\begin{align*}
\frac{dR_{in}}{dt} &= D \left( R_{in} - R \right) + q f l (A_1 + A_2 + A_3 + A_4 + A_5 + A_6 + A_7 + A_8 + A_9 + A_{10}) - \frac{dR}{dt}; \\
\frac{dR_{in}}{dt} &= 5 \cos(0.0002869 \cdot t) \\
\end{align*}
\]

% Compute \( A_{i}/dt \)
\[
\begin{align*}
\frac{dA_{i}}{dt} &= I_m + P_{max} / K_d \log \left( \frac{H_{i} + I_{in}}{H_{i} + I_{out}} \right) \frac{R}{M_{i} + R} \frac{A_{i}}{z} - \left( D + l \right) A_{i} \\
&\quad - \frac{dA_{i}}{dt} - \frac{dA_{i}}{dt} - \frac{dA_{i}}{dt} - \frac{dA_{i}}{dt} - \frac{dA_{i}}{dt} - \frac{dA_{i}}{dt} - \frac{dA_{i}}{dt} - \frac{dA_{i}}{dt}; \\
\end{align*}
\]

% Compute total algal biomass
dATdt = dA1dt + dA2dt + dA3dt + dA4dt + dA5dt + dA6dt + dA7dt + dA8dt + dA9dt + dA10dt;

% Compute total nutrient concentration
dRTdt = q*dATdt + dRdt;

% Put dRTdt, dR/dt, dA1/dt, dA2/dt, dA3/dt, dA4/dt, dA5/dt and dAT/dt into the column vector dS/dt
dSdt = [dA1dt; dA2dt; dA3dt; dA4dt; dA5dt; dA6dt; dA7dt; dA8dt; dA9dt; dA10dt; dATdt; dRdt; dRTdt]; %; dRindt
end