Estimation of effective dilution rate to inhibit cyanobacterial blooms based on a novel competitive growth model -Case study in Lake Tega, Japan

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Abstract

Although water transfer as a functional method to improve water quality and control cyanobacterial blooms in lakes has been used for several decades, there was few studies examining effective dilution rate depending on various water qualities in lakes. It would be due to the scarcity of water transfer execution in fields. Therefore, in order to clarify the optimum dilution rate to suppress cyanobacterial blooms, the competitive growth model based on the Droop model and the Lotka-Volterra model developed for eutrophic conditions was used. First, to verify the wide applicability of the simulation model, a competitive culture experiment between *Microcystis* sp. and *Cyclotella meneghiniana* under limited phosphorus and sufficient nitrogen concentration was conducted, then the cell densities of the two species were predicted by using the simulation model. Results of the competitive experiment revealed that there was no significant discrepancy in the growth of *Microcystis* sp. cell among different dilution groups (p□0.05), while that of *Cyclotella meneghiniana* had significant discrepancy between groups (p□ 0.05), and the accuracy of the simulation model under limited phosphorus concentration was verified. Based on these results, an exact effective dilution rate for the inhibition of *Microcystis* blooms in Lake Tega, Japan, was suggested by this novel simulation model. When the dilution rate reaches 13.3%, the *Microcystis* blooms will hard to occur. The predicted data were also compared with the actual data collected over years in Lake Tega, and its effectiveness has been confirmed.

Introduction

The severe impact of cyanobacterial blooms in eutrophic inland lake on water quality has caused a lot of environmental problems worldwide in recent decades. Many treatment methods such as physical removal, chemical coagulation, sediment dredge, and so on, to improve water quality have been carried out and examined in several studies [1-4]. Water transfer is one of the effective methods among them, not only for ameliorating the water quality but also inhibiting the formation of cyanobacterial blooms. It has been put into practice successfully in many lakes worldwide, such as Lake Valuwe in Netherlands, Lake Moses in America, and Lake Taihu and Lake Xihu in China [5-7]. The mechanism of water transfer is includes washing algae away and diluting or enriching the concentration of nutrients to limit or prompt the algal growth, respectively[8,9]. Though there have been many studies focused on the changes in water quality before and after dilution and the inhibitory effect of cyanobacterial blooms, they still only discussed the specific situation of a certain lake. The results of them were not applicable to other lakes with different water qualities and could not clarify the effective transferring volume of water.

Lake Tega (35° 86' N, 140° 02' E) is a shallow inland eutrophic lake, with the worst water quality from 1974 to 2000 in Japan [10], suffered from cyanobacterial blooms frequently in summer. To improve the deteriorated water quality, a water conveyance channel was constructed in 2000, and a large amount of water (maximum volume: $8.6x10^5$ m^3 day^{-1}) was transferred from the Tone River to Lake Tega via this channel. Since the transfer started in 2000, the concentration of total nitrogen (TN) decreased from the range of 4.0-5.3 mg-N L^{-1} in the 1990s to 2.1-2.2 mg-N L^{-1} in recent five years. The concentration of total phosphorus (TP) also changed, and the maximum value decreased from 0.33 mg-P L^{-1} in the 1990s to

0.16 mg-P L^{-1} in recent five years. The dominant algal species changed into diatoms (mainly the genus *Cyclotella*) instead of cyanobacteria (mainly the genus *Microcystis*), reducing the frequency of cyanobacterial blooms occurrence [10].

Based on the changes in water quality and dominant algal species after water transfer, Amano et al. [11] have examined the effect of phosphorus concentration fluctuation caused by water dilution on the growth of *Microcystis aeruginosa* (strain: UTEX LB 2061) *Cyclotella* sp.(strain: CCAP 1070/4). The result showed that the change of phosphorus concentration could not lead to the replacement of dominant species and the domination of *M. aeruginosa* was always reflected in the outcome of the mixed-species culture experiment, even phosphorus concentration was lowered to 0.01 mg-P L^{-1}. Therefore, it was concluded that the decrease in phosphorus concentration due to the dilution in Lake Tega would be interpreted as a minor factor for the transition of dominant species from *M. aeruginosa* to *Cyclotella* sp. On the contrary, the nitrogen concentration has a great effect on the shift of the dominant species, as the *Cyclotella* sp. completely dominated over *M.aeruginusa* at the nitrate concentrations of 0.5 and 2.5 mg-N L^{-1} in the competitive experiments [8]. One of the possibilities for this could be the higher abilities of nitrogen storage and uptake for *Cyclotella* sp. compared to *M.aeruginusa*, at these two nitrogen concentration conditions. The contribution of different ratio of various nitrogen sources on the growth of *Microcystis* sp. has also been observed by several studies [12,13]. In the north part of Lake Taihu , China, *Microcystis* blooms tented to be dominant during summer, when the molar ratio of ammonium to nitrate was below 1 [14].

Although all the studies mentioned above only discussed the relationship among nutrient concentration, water dilution, and the algal domination transition, there still no exact regularity was drawn by these studies. Sugimoto et al. [9] have concluded that the dilution rate up to 36% per day or more was effective to control cyanobacterial growth according to the result of competitive experiments, but the inhibitory effect of water transfer on the cyanobacterial blooms was not considered when the dilution rate was lower than 36%. Afterward, characteristics of domination for each species under various N(NO_3-N):P (PO_4-P) ratios and dilution rates were predicted by Mikawa et al. [15] based on a competitive growth model. The effective dilution rate to inhibit cyanobacteria was proposed to 20% per day by a simulated result in the study. However, the predicted cell density still had a discrepancy compared with the actual cell density in Lake Tega, due to the shortcoming of the simulation model, especially its overestimation of algal cell density. In order to modify the overestimation problem of algal cell density in this model [16], an improved model has been developed by Chujo et al. [4] , by introducing a growth limitation term from Lotka-Volterra model into the previous model. The developed model presented a more accurate prediction of growth patterns of co-cultured cyanobacteria and diatom, under high nitrogen and phosphorus concentrations.

Though the accuracy of Chujo's model has been confirmed under eutrophic nutrient concentrations [4], the accuracy of the model simulated result under nutrient-limited concentrations was still unclear. In order to reveal a more accurate dilution rate that can effectively inhibit cyanobacterial blooms, it should be

examined whether the Chujo's model is also effective to predict the growth of cyanobacteria and diatom under limited nutrient concentration. If the wide applicability of Chujo's model could be proved, the effective dilution rate would be suggested using this model.

Therefore, in this study, a competitive experiment of two species, *Microcystis* sp. and *Cyclotella meneghiniana*, which were isolated from Lake Tega, was conducted with various dilution rates under phosphorus limited condition. The mechanism of how the dilution affects the shift of the dominant species in the case of low phosphorus concentration was discussed. The growth curves were simulated under the same experimental condition as that of the competitive experiment and the accuracy was tested by comparing with the experimental data. After the accuracy was verified, the growth of the two algal species under simultaneous changes of various nitrogen, phosphorus concentrations, daily renewal rates (which was used to instead dilution rate in semi-continuous culture system) were simulated based on the improved model. According to the simulated values, an effective dilution rate that could suppress the cyanobacteria bloom under the nitrogen and phosphorus concentration of Lake Tega was obtained. The outcome was compared to the growth of cyanobacteria of field observation under different dilution rates in Lake Tega, to discuss the optimum way of diluting lake water for the inhibition of cyanobacterial blooms.

Materials And Methods

Test algae and culture condition

Microcystis sp. and *C. meneghiniana* isolated from Lake Tega [17] were used as test algae in this study. Wright's cryptophytes (WC) medium [18] at pH 8.0 was used as culture medium because it can cultivate both diatoms and cyanobacteria [19]. The initial nitrate-nitrogen (N) and phosphate-phosphorus (P) concentrations of the WC medium were 14 mg-N L^{-1} and 1.55 mg-P L^{-1}, which were adjusted by dissolving sodium nitrate ($NaNO_3$) and dipotassium hydrogen phosphate (K_2HPO_4) in distilled water, respectively. The concentration of silicate-silicon (Si) in medium supplied by sodium metasilicate (Na_2SiO_3) was increased from 2.8 mg-Si L^{-1} to 11 mg-Si L^{-1}, which the same concentration with that in the Tone River water. For subculture, *Microcystis* sp. and *C. meneghiniana* were separately cultured in 100 mL WC medium in a 300 mL Erlenmeyer flask, at 25°C and 135 μmol photons m^{-2} s^{-1} with cool-white fluorescent light with the light-dark circle for 14 hours:10 hours. The both cultured species were transferred and inoculated to fresh medium every two or three weeks. All the media used were sterilized by autoclaving at 121°C for 20 minutes, and both inoculation and sampling transfer were conducted in a clean bench to minimum bacterial contamination.

Growth characteristics of Microcystis *sp.and* C. meneghiniana.

Under sufficient N concentration, the competitive experiment between *M. aeruginosa* and *Cyclotella* sp. showed that the limitation of phosphorus could not lead to the domination of *Cyclotella* sp.[11], which implies that cyanobacteria could still form blooms possibly in actual condition. Meanwhile, the

appropriate dilution rate could inhibit the growth of *M. aeruginosa* effectively. Therefore, to determine the dominant characteristics of *Microcystis* sp. and *C. meneghiniana* under various dilution rates with the phosphorus limitation, a competitive culture experiment was performed with limited phosphorus concentration.

Prior to the competitive experiment, both species were precultured in a nitrogen- and phosphorus-free medium for 7 days to deplete intracellular N and P, so that they would not grow with the intracellular nutrient under nutrient limited condition. In the competitive experiment, both precultured species were inoculated together in the 100 mL sterilized medium in a 300 mL Erlenmeyer flask. The initial cell densities of *Microcystis* sp. and *C. meneghiniana* were adjusted to 1.0×10^4 and 3.98×10^2 cells mL^{-1}, respectively, which were equivalent to the same cell volume of 10^5 μm^3.

In many lakes, there was continuous water inflow from river, which could be modeled as a continuous culture system. The dilution rate (*D*) was used to represent the continuous inflow of the water per day. In this study, the culture medium was diluted with fresh medium once a day, which should be modeled as a semi-continuous culture system. The daily renewal rate (*d*) was used to describe the medium replacement in this culture system. This is because the daily renewal rate (*d*) in the semi-continuous culture system can be converted to the dilution rate (*D*) by the following equation [20] : **see formula 1 in the supplementary files.**

Three experimental groups with different daily renewal rates were set as 0%, 5% and 15%, in the competitive experiment. An appropriate volume of culture medium was removed and as soon an equal volume of fresh medium was added to each flask once a day. In addition to the different daily renewal rates, the P concentration of each group was limited to 0.1 mg-P L^{-1}, which was same as the minimum P concentration in Lake Tega in recent five years [10]. The initial N concentration of 14 mg-N L^{-1} was adequate for the growth of both two species [19]. The cell density and nutrient concentration were measured every 2-5 days and continued until the growth rate became constant. The experiment was conducted in triplicates and the results were presented as [the mean value] ± [standard deviation].

Measurements and statistical analysis

The cell density of samples was measured by counting in a plankton counting plate (MPC-200, Matsunami Glass Industry, Japan) using an optical microscope (ECLIPSE E100, Nikon, Japan) after appropriately diluted.

Concentrations of nitrogen were measured by ion chromatography (ICS-1100, Nippon Dionex, Japan), and molybdenum blue method (Japanese Standard Association, 2016) was used to measure phosphorus concentration. The solution pH was monitored by a pH meter (D-51, Horiba, Japan).

Differences in experimental parameters of *Microcystis* sp. and *C. meneghiniana* in each condition were analyzed by a one-way analysis of variance (ANOVA) with a post hoc comparison being performed with

Turkey's test, via SPSS Statistics (Ver. 23, IBM Corporation, USA). The results were considered to be a significant difference at $p < 0.05$.

Mathematical model and simulation of cyanobacterial bloom appearance

In order to predict the cell densities of *Microcystis* sp. *andC. meneghiniana* and the trends of the appearance of cyanobacterial blooms under the various nutrient concentrations and daily renewal rates, the model constructed by Chujo et al. [4] was used. Then the effective dilution rate for suppressing cyanobacteria was discussed based on the simulated values. The equations of the model are tabulated in Table 1.

The accuracy of Mikawa's model [16] tended to decrease under high nutrient concentrations. Because the growth rate term of the model was formulated based on the Droop equation, the growth rate values in a longer period would be close to μ_{max}, which led to the excess of cell densities. For this reason, the carrying capacity term was introduced in the model by Chujo et al. [4] to limit the growth rate. The way to determine the limiting nutrient in the improved model was also different from that in the previous one. While in Mikawa's model, the limiting nutrient was determined as the relationship between the mass ratio of minimum cell quota of assimilated N:P (the optimum N:P ratio) and the external dissolved N:P mass ratio. The relationship between the mass ratio of cell quota of assimilated N:P (Q_n:Q_p) and the optimum N:P ratio was taken as the determination of the limiting nutrient (as shown in the tag of Table 1) in the Chujo's model.

The model equations were calculated via a fourth-order form of the Runge-Kutta method with the time step of $\Delta t = 0.01$ day, using Microsoft Excel. Furthermore, to investigate the accuracy of the predicted competitive growth patterns, the growth curves of both species were simulated under the same condition as the competitive experiment mentioned above.

In the case of model simulation, the initial N and P concentrations were adjusted from 0 to 5.0 mg-N L^{-1} and 0 to 0.5 mg-P L^{-1}, respectively, reflecting the nutrient concentration in Lake Tega. The daily renewal rate (*d*) was increased from 0% to 20% with a 2.5% interval for each step. Since the two species always reached saturation around 20 days [4], the cell density in the 30th day was used as final result for prediction to ensure the simulated.

Results

Competitive growth characteristics of Microcystis *sp. and* C. meneghiniana *at different daily renewal rates under phosphorus limited condition and prediction*

Competitive growth patterns for *Microcystis* sp.and *C. meneghiniana* in P limited culture experiment are shown in Fig. 1. The simulated growth curves of both species are also depicted in the same figure.

The cell volumes of both species reached saturation within 25 days, at different daily renewal rates (*d*). At *d* = 0%, the cell volume of *Microcystis* sp. was 8.13×10^6 μm^3 L^{-1} at the 24th day, and after that the growth rates remained constant within 7 days. The average growth rate was 0.334 day^{-1} in the initial ten days. After the logarithmic phase, the growth rate began to decrease and maintained a stable value around 0.002 day^{-1} after the 24th day until the end of the experiment. For the other two experimental groups (*d* = 5% and 15%) there was no significant discrepancy in the growth rate at the initial stage and the saturated cell volume among each group (p 0.05), compared to *d* = 0%. On the other hand, the growth rate of *C. meneghiniana* was affected obviously by daily renewal rate in the case of phosphorus limitation. There were significant differences among each group (p 0.05), especially the growth rate after 10 days of these three groups. In the experiment period from the 5th day to the 10th day, the average growth rate at *d* = 5% was 0.167 day^{-1} and then the growth of *C. meneghiniana* remained stationary until the end of the experiment. However, at *d* = 5% and d =15%, the growth of *C. meneghiniana* has come into negative growth after the 10th day. Moreover, the number of saturated cells of *C. meneghiniana* at *d* = 15% decreased by nearly two orders of magnitude compared to that at *d* = 5%.

From the result of nutrient analysis as shown in Fig. 2, it was observed that the dilution had scant effect on the change in nutrient concentration in these experiments. The differences in the N and P concentrations among each group were small, and the decline of both nutrient concentrations were mainly attributed to the growth of both species as the competition experiment progressed. The concentration of P dropped rapidly during the logarithmic phase of the two species and remained at 0.012 mg-P L^{-1} and 0.016 mg-P L^{-1} at *d* = 0% and *d* = 15%, respectively. The concentration of N remained at 8.63 mg-N L^{-1} and 8.62 mg-N L^{-1} at *d* = 0% and *d* = 15%, respectively. From these values, it was observed that the nutrient concentrations were similar values at the end of the cultivation, despite the difference in daily renewal rates.

The simulated growth curves well corresponded with the experimental growth patterns for *Microcystis* sp. The three simulated growth curves almost coincided with each other, and it is consistent with the fact that there was only little difference in experimental data among groups. Thus, the feasibility of Chujo's model under limited phosphorus and sufficient nitrogen conditions could been verified. It would be used to predict the growth of *Microcystis* sp. under various nutrient conditions including phosphorus deficiency. Similar to the case of Microcystis sp., the simulated values also matched with the experimental ones in the growth of *C. meneghiniana* at *d* = 0% under low P concentration. Although a little discrepancy between simulated and experimental data of cell density were observed at *d* = 5% and 15%, the developed model can still be effective to simulate the growth trend of *C. meneghiniana.*

Prediction of Microcystis blooms under various dilution rates

Since the accuracy of the model was verified, the cell density of *Microcystis* sp. was predicted with the N and P concentrations in Lake Tega before and after water transfer. The estimated *Microcystis* sp. cell densities were 2.72×10^6 cells mL^{-1} and 1.36×10^6 cells mL^{-1}, respectively. Based on these values, it could be assumed that when the predicted cell density was more than 2.72×10^6 cells mL^{-1}, there is a

high possibility of cyanobacterial blooms occurrence, while when the predicted value was less than 1.36 × 10^6 cells mL^{-1}, the cyanobacterial blooms would occur hardly. The plane view of contour figures in Fig.3 shows the predicted values at different daily renewal rate. The dark grey area was taken as the bloom area where the predicted cell densities were equal to or more than 2.72 × 10^6 cells mL^{-1}. The light grey area and the white-grey area were taken as the non-bloom area where the predicted cell densities equal to or less than 1.36 × 10^6 cells mL^{-1}. The dashed lines were used to identify different orders of magnitude. The solid lines were used to indicate the range of the bloom area.

When the daily renewal rate changed from 0% to 5%, the bloom area was obviously enlarged. However, as the renewal rate gradually increased from 5%, the bloom area gradually decreased, at the same time, the non-bloom area increased. At a certain dilution rate, the cyanobacterial blooms area would disappear. In particular, it can be found in the figures that when the renewal rate was equal to or higher than 12.5%, the bloom area no longer existed. Based on Eq.1, the dilution rate D was 13.3% when the renewal rate was 12.5%.

The data from Chiba prefectural government [10] was used to calculate the annual average of dilution rate and the cell densities of *Microcystis* sp. in every month of each year in the Lake Tega. The results were shown in Fig. 4. The actual results indicated that when the dilution rate was above 13.3%, *Microcystis* sp. was hard to proliferate in Lake Tega, and the cell density was generally less than 3 × 10^3 cells mL^{-1}. This trend apparently corresponds to the experimental data shown in Fig.3. Thus, the dilution rate D = 13.3% could be considered to inhibit cyanobacterial blooms effectively, which the simulation results in this study was consistent with.

Discussion

The relationship between phosphorus concentration and algal growth, and also the occurrence of algal blooms have been studied in many studies [2,21,22]. The decrease of phosphorus concentration caused by water transfer has been proven that it cannot lead to the shift of dominant algal species and inhibit the formation of cyanobacterial blooms. [2,11]. In this study, *Microcystis* sp. showed a better adaptability than *C. meneghiniana* under the phosphorus limited condition. The growth patterns obtained from monocultured experiment of the two species in previous study[4] indicate that the maximum cell quota (Q_{max}) of *C. meneghiniana* for N and P ($Q_{max,n}$ = 104.00 pg $cell^{-1}$, $Q_{max,p}$ = 5.08 pg $cell^{-1}$) were nearly 20 times higher than those of *Microcystis* sp. ($Q_{max,n}$ = 5.00 pg $cell^{-1}$, $Q_{max,p}$ = 0.28 pg $cell^{-1}$), whereas the uptake parameters (ρ) for nitrogen were only two times that of *Microcystis* sp. This indicates that the deficiency of phosphorus would influence the growth of *C. meneghiniana* more than *Microcystis* sp. and the *Microcystis* sp. would grow more advantageously with adequate nutrient, excluding the effect of other factors. Based on the changes of nutrient concentration shown in Fig.2, there should be no significant differences in cell densities of both species in each group. However, the *C. meneghiniana* cell densities decreased significantly with the increase of daily renewal rate. Thus, it would be considered that the

number of *C. meneghiniana* cells washed away was greater than the growth rate under the phosphorus limitation.

Tatsumoto et al. [23] indicated that the ignition loss of the Lake Tega sediment was measured to be ca. 16%, and the upper 20 cm of the sediment was supposed to contribute to the nutrient elution, which may provide nutrient constantly after water transfer. The pH is also an important influential factor of the nutrient release from sediment [24], though the release of ammonium nitrogen increases with pH and the release of nitrate nitrogen has no obvious relation with pH [25,26]. The release of phosphorus will decrease with pH increasing until it reaches 7.0, and the releasement will increase with pH after it is higher than 8.0 [27]. Therefore, methods controlling the source of pollutants, adjusting the nutrient composition, and controlling the pH of the water body can be considered for the prevention and management of cyanobacterial blooms in the future.

As for the model simulation, the prediction of *Microcystis* sp. growth shows a reverse decrease at the daily renewal rates of lower than 5%. It was predicted that the occurrence of cyanobacteria blooms was nearly impossible when the daily renewal rate was 0%. However, in reality, the smaller the daily renewal rate is, the more possibility the cyanobacterial blooms occurrence should be [28]. The problem would be due to a shortcoming with the nutrient uptake term of Chujo's model. According to the equations of the current simulation model, the uptake rate term was always taken as ρ_{max} when the nutrient concentration was adequate. However, it could not always reach the maximum value and would decrease with algae growth and the decrease of nutrient concentrations in competitive experiment process. As a result of current equations, the nutrient concentration should decrease exponentially when the cell densities of *Microcystis* sp. increase exponentially. However, in reality, when sufficient nutrients were present, the densities of cells increase exponentially, while the decrease in nutrient concentration was only proportionally reduced. [4,29]. For this reason, the predicted uptake of nutrients of *Microcystis* sp. after the logarithmic phase would be overestimated.

However, when the two species were grown under eutrophic conditions, *C. meneghiniana* showed a very advantage in nutrient uptake over *Microcystis* sp. based on the nutrient uptake characteristics as shown in our previous study [4]. At the daily renewal rate of 0%, both the simulated results and the experimental patterns indicated that the nutrient was almost exclusively occupied by *C. meneghiniana*, which led to the inhibition of the proliferation of *Microcystis* sp. That provided a reasonable explanation and support for the predicted cell density of *Microcystis* sp. at d = 0%. But there was still a gap between the predicted value and the experimental value of the growth of *C. meneghiniana*, when it was under the relatively scarce nutrient concentration. In order to improve the accuracy of simulation, the amelioration of the uptake rate and the other environmental factors such as temperature and light intensity should be focused on in future study.

Summary

Depending on the results of competitive experiment under the P limited and N sufficient conditions, it was indicated that low concentration of P restricted both the growth of *C. meneghiniana* and *Microcystis* sp. Under the P limitation, the dilution of medium affected the growth of *C. meneghiniana* more than that of *Microcystis* sp., by washing the *C. meneghiniana* cells away with renewal medium. The Chujo's improved simulation model used in the study was also proven that it still had good accuracy even under P limited conditions by comparing the simulated cell densities of the two species with experimental values. According to the simulated results calculated by the simulation model, the effective minimum dilution rate inhibiting *Microcystis* sp. was found to be D = 13.3% under the experimental conditions, and this conclusion was strongly consistent with the actual survey data in Lake Tega. Based on the accuracy of the simulated value, the Chujo's model can be considered to simulate the growth of cyanobacteria more accurately under both eutrophic nutrient concentrations and limited nutrient concentrations, and can serve as a powerful tool to apply for the management of many eutrophic lakes.

Declarations

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Code availability: Not applicable.

Author's contribution: Jingnan Li and Masato Chujo designed and performed the experiments, derived the models and analyzed the data. All authors contributed to the final version of the manuscript. Yoshimasa AMANO and Motoi MACHIDA supervised the project.

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Nomenclature

N Nitrogen concentration (mg-N L^{-1})

N_0 Initial nitrogen concentration (mg-N L^{-1})

P Phosphorus concentration (mg-P L^{-1})

P_0 Initial phosphorus concentration (mg-P L^{-1})

S Substrate (mg L^{-1})

C Cell density (cells mL^{-1})

Q Cell quota (pg $cell^{-1}$)

N_0 Initial nitrogen concentration (mg-N L^{-1})

P_0 Initial phosphorus concentration (mg-P L^{-1})

ρ_{max} Maximum uptake rate（pg $cell^{-1}$ day^{-1}）

ρ_{max}^{hi} Maximum uptake rate at the beginning of cultivation (pg $cell^{-1}$ day^{-1})

ρ_{max}^{lo} Maximum uptake rate at the maximum growth rate (pg $cell^{-1}$ day^{-1})

K_μ Half-saturation constant for growth rate (mg L^{-1})

K_ρ Half-saturation constant for uptake rate (mg L^{-1}）

K_ρ^{hi} Half-saturation constant for uptake rate at the beginning of cultivation (mg L^{-1})

K_ρ^{lo} Half-saturation constant for uptake rate at the maximum growth rate (mg L^{-1})

μ_{max} Maximum growth rate (day^{-1})

μ'_{max} Maximum specific growth rate (day^{-1})

Q_{min} Minimum cell quota (pg $cell^{-1}$)

Q_{max} Maximum cell quota (pg $cell^{-1}$)

D Dilution rate (day^{-1})

d Daily renewal rate (day^{-1})

a Inter-specific competition rate

Subscripts A and B refer to *Microcystis* sp. and *Cyclotella meneghiniana*, respectively

Subscripts n and p refer to nitrogen and phosphorus, respectively

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Table

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