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ORIGINAL PAPER

# Mathematical analysis on nonautonomous droop model for phytoplankton growth in a chemostat: boundedness, permanence and extinction

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**Abstract** In this paper, we considered the non-autonomous Droop model for phytoplankton growth in a chemostat in which the nutrient input varies non-periodically. It is assumed that growth rate varies with the internal nutrient level of the cell and the uptake rate of phytoplankton depends on both the external and the internal nutrient concentrations. A series of new criteria on the positivity, boundedness, permanence and extinction of the population is established.

**Keywords** Chemostat · Droop model · Phytoplankton · Positivity · Boundedness · Permanence · Extinction

## 1 Introduction

The chemostat is an important laboratory apparatus used to culture microorganisms. See [4,5,12,14], and [22–25] for a detailed description of a chemostat and for various mathematical models for analyzing chemostat models.The Droop model (see [2,3]) of phytoplankton growth in a chemostat has been widely investigated in many literatures (see [7–10]). As in Monod [10], the classical chemostat equations modeling phytoplankton population dynamics originally related the growth rate of the cells to the nutrient concentration in the medium. It is assumed that the nutrient uptake rate is proportional to the rate of reproduction. The constant of proportionality which converts units of nutrient to units of organisms is called the yield constant. Because of the assumed constant value of the yield, the classical Monod model is refereed to as the constant-yield model by Grover [9].

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Droop [2] observed that under nonequilibrium correlations the nutrient concentration in the chemostat remained relatively high at the low dilution rates, a phenomenon that cannot be explained by the Monod model. This led him to introduce the notion of an internal nutrient pool and to propose that nutrient uptake is function of the ambient nutrient concentration while growth rate varies with the internal nutrient level of the cell, called the cell quota, which may be viewed as the average amount of stored nutrient in each cell of the particular organism in the chemostat. The cell quota increases due to nutrient uptake and decreases duo to cell division, which acts to spread the total stored nutrient uptake over more cells. Grover [7,9] refereed to the Droop model as the variable-yield or the the variable-nutrient stored model.

There has been a great deal of current interest among phytoplankton ecologists in both experimental and theoretical analysis of nutrient-limited phytoplankton growth and competition studies in variable-nutrient environments (see Smith [13], Grover [7,8] and Sommer [11]). There are number of different operating parameters in the Droop model in addition to the feed-nutrient concentration which might be interesting to vary with time in a periodic manner (see Butler, Hsu and Waltman [1], Stephanopoulos et al. [16], Smith [14,15], Smith and Waltman [12]). Smith [14] studied the dynamics of the Droop model incorporating a periodically varying nutrient input which takes the following forms

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= N(\mu(Q) - D), \\ \frac{\mathrm{d}Q}{\mathrm{d}t} &= \rho(S, Q) - \mu(Q)Q, \\ \frac{\mathrm{d}S}{\mathrm{d}t} &= D(S^0(t) - S) - N\rho(S, Q), \end{aligned} \tag{1}$$

where the nutrient input $S^0(t)$, uptake rate of nutrient by phytoplankton cells $\rho(S, Q)$ and the growth rate of phytoplankton population $\mu(Q)$ varies periodically. In [14], the author proved that the periodically forced Droop model (1) has precisely two dynamic regimes depending on a threshold condition involving the dilution rate. If the dilution rate is such that the sub-threshold condition hold, the phytoplankton population is washed out of the chemostat. If the super-threshold condition holds, then there is a unique periodic solution to which all solutions approach asymptotically.

Stimulated by the work of [14], we introduce the following more general case of model (1):

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= N(\mu_1(t, Q) - D(t)), \\ \frac{\mathrm{d}Q}{\mathrm{d}t} &= \rho_1(t, S, Q) - \mu_2(t, Q)Q, \\ \frac{\mathrm{d}S}{\mathrm{d}t} &= a(t) - b(t)S - N\rho_2(t, S, Q), \end{aligned} \tag{2}$$

where $S(t)$ denotes the concentration of the nutrient and $N(t)$ denotes the concentration of the phytoplankton cells in the culture vessel; Q(t) denotes the internal nutrient level of the cells, called the cell quota, which may be viewed as the average amount of stored nutrient in each cell of the particular organism in the chemostat; The $\rho_1(t, S, Q)$ represents the per unit biomass uptake rate of nutrient by phytoplankton cells and $\rho_2(t, S, Q)$ denotes the consumption rate of phytoplankton cells at time $t$; $\mu_1(t, Q)$ describes the per unit biomass growth rate and $\mu_2(t, Q)$ denotes the removal rate. $a(t)$ and $b(t)$ are the input nutrient concentration and the dilution rate, respectively, and $D(t)$ represents the specific removal rate (it equals to sum of death rate and washout rate of the population $N(t)$).

The aim of this paper is to discuss the positivity, boundedness, permanence and extinction of the all species for model (2) and establish a series of very interesting criteria. The methods used in this paper are motivated by the works on the uniform persistence for the periodic predator-prey Lotka–Volterra models in [18], the permanence and extinction for the periodic predator-prey systems in patchy environment with delay in [20] and the permanence criteria in nonautonomous predator-prey Kolmogorov systems and its applications in [21].

The organization of this paper as follows. In the next section, we introduce several assumptions for model (2) and the definitions of the permanence and extinction of species. Further, we will give two lemmas which will be essential to our proofs and discussions. Positivity and boundedness of solutions of model (2) are discussed in Sect. 3. In Sect. 4, the results on the permanence and strong persistence of solutions of model (2) are stated and proved. At last, in Sect. 5 the results on the extinction of solutions of model (2) will be stated and proved.

## 2 Preliminaries

We denote $R_+ = (0, \infty)$, $R_{+0} = [0, \infty)$, $R_+^2 = R_+ \times R_+$, $R_{+0}^2 = R_{+0} \times R_{+0}$, $R_+^3 = R_+ \times R_+ \times R_+$ and $R_{+0}^3 = R_{+0} \times R_{+0} \times R_{+0}$. In this paper, for model (2) we always assume that the following condition holds.

($H_1$) Functions $a(t)$ and $b(t)$ are bounded and continuous defined on $R_{+0}$, $\inf_{t \in R_+} a(t) \geq 0$ and there is a constant $\omega > 0$ such that

$$\liminf_{t\to\infty} \int_t^{t+\omega} a(s)\mathrm{d}s > 0, \quad \liminf_{t\to\infty} \int_t^{t+\omega} b(v)\mathrm{d}v > 0.$$

Assumption ($H_1$) shows that, when time $t$ is large enough, the growth rate of the nutrient and the dilution rate of the nutrient on interval $[t, t+\omega]$ are strictly positive.

Putting $N = 0$ in the last equation of model (2), we obtain

$$\frac{\mathrm{d}S}{\mathrm{d}t} = a(t) - b(t)S. \tag{3}$$

Let constant $\alpha_0 > 0$. For any constant $\alpha \in [-\alpha_0, \alpha_0]$ and a bounded continuous function $c(t) : R_{+0} \to R$, we further consider the following equation

$$\frac{\mathrm{d}S}{\mathrm{d}t} = a(t) + \alpha c(t) - b(t)S. \tag{4}$$

For any initial point $(t_0, S_0) \in R_{+0} \times R_+$. Let $S^*(t)$ and $S_\alpha(t)$ be the solutions of systems (3) and (4) satisfying the initial conditions $S^*(t_0) = S_0$ and $S_\alpha(t_0) = S_0$, respectively. Using a similar argument as in [19], we can prove the following result.

**Lemma 1** *Suppose that $(H_1)$ holds. Then we have*

*(a) There are constants $M_1 > 1$ and $0 < \gamma_0 < 1$ such that for any $(t_0, S_0) \in R_{+0} \times R_+$ and $\alpha \in [-\gamma_0, \gamma_0]$*

$$M_1^{-1} \le \liminf_{t\to\infty} S^*(t) \le \limsup_{t\to\infty} S^*(t) \le M_1,$$

*and*

$$M_1^{-1} \le \liminf_{t\to\infty} S_\alpha(t) \le \limsup_{t\to\infty} S_\alpha(t) \le M_1.$$

*(b) $S_\alpha(t)$ is globally uniformly attractive on $[t_0, \infty)$.*
*(c) $S_\alpha(t)$ converges to $S^*(t)$ uniformly for $t \in [t_0, \infty)$ as $\alpha \to 0$.*

Let $S^*(t)$ be some fixed positive solution of system (3) with initial value $S^*(0) = S_0^* > 0$. For model (2), we introduce the following assumptions.

$(H_2)$ Function $\rho_1(t, S, Q)$ satisfies the following conditions:

(a) $\rho_1(t, S, Q)$ is continuous, $\rho_1(t, S, Q) \ge 0$ and $\rho_1(t, 0, 0) = 0$ for all $(t, S, Q) \in R^3_{+0}$; $\rho_1(t, S^*(t), 0)$ is bounded on $t \in R_{+0}$.
(b) The derivative $\frac{\partial \rho_1(t,S,Q)}{\partial S}$ and $\frac{\partial \rho_1(t,S,Q)}{\partial Q}$ exist, $\frac{\partial \rho_1(t,S,Q)}{\partial S} \ge 0$ and $\frac{\partial \rho_1(t,S,Q)}{\partial Q} \le 0$ for all $(t, S, Q) \in R^3_{+0}$; for any constant $\eta > 0$, $\frac{\partial \rho_1(t,S,Q)}{\partial S}$ is bounded on $(t, S, Q) \in R_{+0} \times [0, \eta] \times [0, \eta]$.
(c) There is a constant $k_1 > 0$ such that $\liminf_{t\to\infty} \int_t^{t+\omega} \rho_1(u, S^*(u), k_1) du > 0$.

$(H_3)$ Function $\rho_2(t, S, Q)$ satisfies the following conditions:

(a) $\rho_2(t, S, Q)$ is continuous, $\rho_2(t, S, Q) \ge 0$ and $\rho_2(t, 0, 0) = 0$ for all $(t, S, Q) \in R^3_+$; for any positive constants $\alpha$ and $\beta$, $\rho_2(t, \alpha, \beta)$ is bounded on $t \in R_{+0}$ and $\liminf_{t\to\infty} \rho_2(t, \alpha, \beta) > 0$.
(b) The derivative $\frac{\partial \rho_2(t,S,Q)}{\partial S}$ and $\frac{\partial \rho_2(t,S,Q)}{\partial Q}$ exist, $\frac{\partial \rho_2(t,S,Q)}{\partial S} \ge 0$ and $\frac{\partial \rho_2(t,S,Q)}{\partial Q} \le 0$ for all $(t, S, Q) \in R^3_{+0}$; for any constants $\eta > 0$, $\frac{\partial \rho_2(t,S,0)}{\partial S}$ is bounded on $(t, S) \in R_{+0} \times [0, \eta]$.

$(H_4)$ Function $\mu_1(t, Q)$ satisfies the following conditions:

(a) $\mu_1(t, Q)$ is continuous and $\mu_1(t, 0) = 0$ for all $(t, S) \in R^2_{+0}$; for any constant $\sigma > 0$, $\mu_1(t, \sigma)$ is bounded on $t \in R_{+0}$.
(b) The derivative $\frac{\partial \mu_1(t,Q)}{\partial Q}$ exists and $\frac{\partial \mu_1(t,Q)}{\partial Q} \ge 0$ for all $(t, Q) \in R^2_{+0}$; for any constant $\alpha > 0$, $\frac{\partial \mu_1(t,Q)}{\partial Q}$ is bounded on $(t, Q) \in R_{+0} \times [0, \alpha]$.

($H_5$) Function $\mu_2(t, Q)$ satisfies the following conditions:

(a) $\mu_2(t, Q)$ is continuous and $\mu_2(t, 0) = 0$ for all $(t, S) \in R^2_{+0}$; for any constant $\sigma > 0$, $\mu_2(t, \sigma)$ is bounded on $t \in R_{+0}$ and $\liminf_{t\to\infty} \int_t^{t+\sigma} \mu_2(s, k_2)\mathrm{d}s > 0$.

(b) The derivative $\frac{\partial \mu_2(t,Q)}{\partial Q}$ exists for all $(t, Q) \in R^2_{+0}$ and there is a nonnegative continuous function $q(t)$, satisfying $\liminf_{t\to\infty} \int_t^{t+\omega} q(s)\mathrm{d}s > 0$, and a continuous function $p(u)$, satisfying $p(u) > 0$ for all $u \in R_+$, such that

$$\frac{\partial \mu_2(t, Q)}{\partial Q} \geq q(t)p(Q) \quad \text{for all} \quad (t, Q) \in R^2_{+0}.$$

($H_6$) Function $D(t)$ is bounded and continuous on $R_{+0}$ and there is a constant $\omega > 0$ such that $\liminf_{t\to\infty} \int_t^{t+\omega} D(s)\mathrm{d}s > 0$.

**Remark 1** Assumptions ($H_2$) and ($H_3$) show that the uptake rate of the nutrient by phytoplankton cells $\rho_1(t, S, Q)$ and assumption rate of the nutrient by phytoplankton cells $\rho_2(t, S, Q)$ are strictly increasing with nutrient concentration S, nonincreasing with cell quota Q, and to vanish in the absence of nutrient and cell quota. In other words, an increase in the ambient nutrient concentration with no change in cell quota leads to a greater uptake rate and consumption rate, while an increase in the internal pool with no change in ambient nutrient concentration can only decrease the uptake rate and consumption rate. In ($H_2$) we see that, when time $t$ is large enough and nutrient reach the available nutrient and the cell quota keep a constant value, the values of the uptake rate of the phytoplankton on interval $[t,\ t + \omega]$ are strictly positive.

In assumptions ($H_4$) and ($H_5$), we see that, when the concentration of the cell quota increases, the per capita growth rate of phytoplankton cell $\mu_1(t, Q)$ and removal rate of cell quota $\mu_2(t, Q)$ are increasing and vanish in the absence of cell quota; The phytoplankton growth rate $\mu_1(t, Q)$ and the racial rate of the phytoplankton growth rate to the cell quota are limited when cell quota keep constant; when time $t$ is large enough and the cell quota keep a constant value, the values of the the removal rate of the cell quota on interval $[t,\ t + \omega]$ are strictly positive.

Assumption ($H_6$) shows that when time $t$ is large enough, the values of the sum of death rate and washout rate of the population $N(t)$ on interval $[t, t + \omega]$ are strictly positive.

Let $(N(t), Q(t), S(t))$ be any solution of model (2). If $N(t) > 0$, $Q(t) > 0$ and $S(t) > 0$ on its maximal existence interval, then such solution is called to be positive. The definitions of permanence, persistence and extinction of population have been given in many articles (see, for example, [6,17]). Here, for the requirement of this paper we give the following statements.

**Definition 1** Let $(N(t), Q(t), S(t))$ be any positive solution of model (2).

(a) Plankton population $N$ is said to be strongly persistent, if $\liminf_{t\to\infty} N(t) > 0$.

(b) Plankton population $N$ is said to be permanent, if there are constants $M \geq m > 0$, and $M$ and $m$ are independent of any positive solution of model (2), such that $m \leq \liminf_{t\to\infty} N(t) \leq \limsup_{t\to\infty} N(t) \leq M$.

(c) Plankton population $N$ is said to be extinct, if $\lim_{t\to\infty} N(t) = 0$.

Similarly, we can give the definitions of strong persistence, permanence and extinction of nutrients $S$ and $Q$. We here omit them.

Putting $S(t) = S^*(t)$ in the second equation of model (2), we obtain

$$\frac{\mathrm{d}Q}{\mathrm{d}t} = \rho_1(t, S^*(t), Q) - \mu_2(t, Q)Q. \tag{5}$$

Since $\inf_{t\in R_{+0}} S^*(t) > 0$ by Lemma 1, we can choose a constant $\alpha_0 > 0$ such that $\inf_{t\in R_{+0}} S^*(t) - \alpha_0 > 0$. For any $\alpha \in [-\alpha_0, \ \alpha_0]$, we further consider the following equation

$$\frac{\mathrm{d}Q}{\mathrm{d}t} = \rho_1(t, S^*(t) + \alpha, Q) - \mu_2(t, Q)Q. \tag{6}$$

For any initial point $(t_0, Q_0) \in R_{+0} \times R_+$, let $Q^*(t)$ and $Q_\alpha(t)$ be the solutions of systems (5) and (6) satisfying the initial conditions $Q^*(t_0) = Q_0$ and $Q_\alpha(t_0) = Q_0$, respectively. We have the following result.

**Lemma 2** *Suppose that* $(H_1)$, $(H_2)$ *and* $(H_5)$ *hold. Then we have*

*(a) there are constants* $M_2 > 1$ *and* $0 < \gamma_0 < 1$ *such that for any* $(t_0, Q_0) \in R_{+0} \times R_+$ *and* $\alpha \in [-\gamma_0, \ \gamma_0]$

$$M_2^{-1} \le \liminf_{t\to\infty} Q^*(t) \le \limsup_{t\to\infty} Q^*(t) \le M_2,$$

*and*

$$M_2^{-1} \le \liminf_{t\to\infty} Q_\alpha(t) \le \limsup_{t\to\infty} Q_\alpha(t) \le M_2;$$

*(b)* $Q_\alpha(t)$ *is globally uniformly attractive on* $[t_0, \ \infty)$*;*
*(c)* $Q_\alpha(t)$ *converges to* $Q^*(t)$ *uniformly for* $t \in [t_0, \ \infty)$ *as* $\alpha \to 0$.

*Proof* On the basis of $(\mathrm{H}_1)$ and $(\mathrm{H}_4)$, conclusion $(a)$ can be proved by using a similar argument as in [22, Lemma 1].

Now, we prove conclusion $(b)$. For any constant $\eta > 1$ and $\bar{t}_0 \in [t_0, \ \infty)$, let $\bar{Q}_\alpha(t)$ be a solution of system (6) with initial value $\bar{Q}_\alpha(\bar{t}_0) \in [\eta^{-1}, \ \eta]$ . By conclusion $(a)$, there are constants $M_0 > 1$ and $0 < \gamma_0 < 1$ such that for any $\alpha \in [-\gamma_0, \ \gamma_0]$

$$M_0^{-1} \le Q^*(t) \le M_0, \quad M_0^{-1} \le Q_\alpha(t) \le M_0 \quad \text{for all} \quad t \ge t_0. \tag{7}$$

Consider Liapunov function $V(t) = |\ln \bar{Q}_\alpha(t) - \ln Q_\alpha(t)|$. Calculating the Dini derivative $D^+V(t)$, by ($H_2$) and ($H_5$) we obtain

$$\begin{aligned} D^+V(t) &= \mathrm{sign}(\bar{Q}_\alpha(t) - Q_\alpha(t))[\bar{Q}_\alpha^{-1}(t)\rho_1(t, S^*(t), \bar{Q}_\alpha(t)) \\ &\quad - Q_\alpha^{-1}(t)\rho_1(t, S^*(t), Q_\alpha(t)) - \mu_2(t, \bar{Q}_\alpha(t)) + \mu_2(t, Q_\alpha(t))] \\ &\le \mathrm{sign}(\bar{Q}_\alpha(t) - Q_\alpha(t))[\mu_2(t, Q_\alpha(t)) - \mu_2(t, \bar{Q}_\alpha(t))] \\ &= -\frac{\partial \mu_2(t, \xi(t))}{\partial Q}|Q_\alpha(t) - \bar{Q}_\alpha(t)| \\ &\le -q(t)p(\xi(t))|Q_\alpha(t) - \bar{Q}_\alpha(t)|, \end{aligned} \tag{8}$$

for all $t \ge \bar{t}_0$, where $\xi(t)$ is situated between $Q_\alpha(t)$ and $\bar{Q}_\alpha(t)$. Hence $V(t) \le V(t_0)$ for all $t \ge \bar{t}_0$. Consequently, by (7) we have

$$|\ln \bar{Q}_\alpha(t)| \le |\ln Q_\alpha(t)| + V(t_0) \le \ln(\eta M_0^2),$$

for all $t \ge \bar{t}_0$. Hence $\eta^{-1}M_0^{-2} \le Q_\alpha(t) \le \eta M_0^2$ for all $t \ge \bar{t}_0$. Further by (7), we obtain

$$\eta^{-1}M_0^{-2}V(t) \le |Q_\alpha(t) - Q_\alpha^*(t)| \le \eta M_0^{-2}V(t),$$

for all $t \ge \bar{t}_0$. Consequently, by (8) it follows that

$$D^+V(t) \le -M_0^{-1}\eta^{-1}q(t)p(\xi(t))V(t) = -q(t)M_3V(t) \quad \text{for all} \quad t \ge \bar{t}_0, \tag{9}$$

where $M_3 = M_0^{-1}\eta^{-1}\min\{p(Q) : \eta^{-1}M_0^{-2} \le Q \le \eta M_0^2\}$.

Since $\liminf_{t\to\infty} \int_t^{t+\omega} q(u)\mathrm{d}u > 0$, we can choose positive constants $\delta$ and $T_1$ such that

$$\int_t^{t+\omega} q(u)du \ge \delta \quad \text{for all} \quad t \ge T_1.$$

Let $T_1' = \bar{t}_0 + T_1$. For any $t \ge T_1'$, there is an integer $n_t \ge 0$ such that $t \in [T_1' + n_t\omega, T_1' + (n_t + 1)\omega)$. Integrating (9) from $T_1'$ to $t$, we have

$$\begin{aligned} V(t) &\le V(T_1')\exp\int_{T_0'}^{t}(-M_0q(u))\mathrm{d}u \\ &= V(T_1')\exp\left[\int_{T_0'}^{T_1'+\omega} + \cdots + \int_{T_0'+n_t\omega}^{t}\right](-M_0q(u))\mathrm{d}u \\ &\le V(T_1')\exp(-M_3\delta n_t). \end{aligned}$$

Since $V(T_1') \le V(\bar{t}_0) \le \ln(\eta M_0)$, we further have

$$\begin{aligned} V(t) &\le \ln(\eta M_0)\exp[-M_3\delta\omega^{-1}(t - T' - \omega)] \\ &= M^*\eta\exp[-M_3\delta\omega^{-1}(t - t_0)], \end{aligned} \tag{10}$$

where $M^* = \ln(\eta M_0)\exp[M_3\delta(1 + \frac{T_1'}{\omega})]$. Hence, for any constant $\epsilon > 0$, from (10), there is a large enough $T(\eta, \epsilon) \ge T_1'$ such that

$$V(t) < \frac{\epsilon}{\eta M_0^2} \quad \text{for all} \quad t \ge \bar{t}_0 + T(\eta, \epsilon).$$

Therefore, $|Q_\alpha(t) - \bar{Q}_\alpha(t)| < \epsilon$ for all $t \ge \bar{t}_0 + T(\eta, \epsilon)$. This shows that solution $Q_\alpha(t)$ is globally uniformly attractive on $[t_0, \infty)$.

Finally, we prove conclusion $(c)$. By conclusion $(a)$ of Lemma 1, we have $M_4^{-1} \le S^*(t) \le M_4$ for all $t \in R_{+0}$, where $M_4$ is some positive constant. Let $V(t) = |\ln Q_\alpha(t) - \ln Q^*(t)|$, calculating the Dini derivative, by $(H_2)$ and $(H_5)$ we obtain

$$\begin{aligned} D^+V(t) &= \text{sign}(Q_\alpha(t) - Q^*(t))[Q_\alpha^{-1}\rho_1(t, S^*(t) + \alpha, Q_\alpha(t)) - \mu_2(t, Q_\alpha(t)) \\ &\quad - Q^{*-1}(t)\rho_1(t, S^*(t), Q^*(t)) + \mu_2(t, Q^*(t))] \\ &= \text{sign}(Q_\alpha(t) - Q^*(t))[Q_\alpha^{-1}(t)\rho_1(t, S^*(t) + \alpha, Q_\alpha(t)) \\ &\quad - Q_\alpha^{-1}(t)\rho_1(t, S^*(t), Q_\alpha(t)) + Q_\alpha^{-1}(t)\rho_1(t, S^*(t), Q_\alpha(t)) \\ &\quad - Q^{*-1}(t)\rho_1(t, S^*(t), Q^*(t)) + \mu_2(t, Q^*(t)) - \mu_2(t, Q_\alpha(t))] \\ &\le -\frac{\partial\mu_2(t, \xi_1(t))}{\partial Q}|Q_\alpha(t) - Q^*(t)| + Q_\alpha^{-1}(t)|\frac{\partial\rho_1(t, \xi_2(t), Q_\alpha(t))}{\partial S}\alpha| \\ &\le -q(t)p(\xi_1(t))|Q_\alpha(t) - Q^*(t)| + M_5|\alpha| \\ &\le -q(t)p(\xi_1(t))M_0^{-1}V(t) + M_5|\alpha| \\ &\le -q(t)p_0V(t) + M_5|\alpha|, \end{aligned} \tag{11}$$

where $\xi_1(t))$ is situated between $Q_\alpha(t)$ and $Q^*(t)$, $\xi_2(t)$ situated between $S^*(t) + \alpha$ and $S^*(t)$, $p_0 = M_0^{-1}\min\{p(Q) : M_0^{-1} \le Q \le M_0\}$ and

$$M_5 = \sup\left\{\left|\frac{\partial\rho_1(t, S, Q)}{\partial S}\right| Q^{-1} : t \in R_{+0}, S \in [M_4^{-1}, M_4 + \gamma_0], Q \in [M_0^{-1}, M_0]\right\}.$$

Since $M_5 < \infty$, $\liminf_{t\to\infty}\int_t^{t+\omega} q(u)\mathrm{d}u > 0$ and $Q_\alpha(t_0) = Q^*(t_0)$, by the comparison theorem and the variation of constants formula of solutions for first-order linear differential equations we can obtain from (11) that $V(t) \to 0$ uniformly for $t \in [t_0, \infty)$ as $\alpha \to 0$. Since

$$|Q_\alpha(t) - Q^*(t)| \le M_0V(t) \quad \text{for all} \quad t \in [t_0, \infty),$$

we finally have that $Q_\alpha(t) \to Q^*(t)$ uniformly for $t \in [t_0, \infty)$ as $\alpha \to 0$. This completes the proof.

## 3 Positivity and boundedness

For any $z_0{=}(N_0, Q_0, S_0) \in R^3_+$, we denote by $z(t, z_0){=}(N(t, z_0), Q(t, z_0), S(t, z_0))$ the solution of model (2) with initial condition $z(0, z_0) = z_0$. On the positivity of solutions of model (2) we have the following result.

**Theorem 1** *Suppose that* $(H_1) - (H_6)$ *hold. Let* $z(t) = (N(t), Q(t), S(t))$ *be a solution of model (2) with initial condition* $z(0) = (N(0), Q(0), S(0))$. *If* $z(0) \in R^3_+$, *then* $z(t) > 0$ *for all* $t \in R_{+0}$.

*Proof* Let $I = [0, t_1)$ be the maximal interval such that $z(t) = (N(t), S(t), Q(t))$ exists and is positive for all $t \in I$. Obviously, $t_1 > 0$. We will prove $t_1 = \infty$. Suppose $t_1 < \infty$. Then we must have either $\lim_{t\to t_1} \min\{S(t), Q(t), N(t)\} = 0$ or $\lim_{t\to t_1} \max\{S(t), Q(t), N(t)\} = \infty$. From model (2) we have

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} \le a(t) - b(t)S(t) \quad \text{for all} \quad t \in I.$$

Using the comparison principle and conclusion $(a)$ of Lemma 2 for $\alpha = 0$, we obtain that $S(t)$ is bounded on $I$, say $0 < S(t) \le S_1$ for all $t \in I$, where $S_1$ is some positive constant. Further from model (2) we also have

$$\frac{\mathrm{d}Q(t)}{\mathrm{d}t} \ge -\mu_1(t, Q(t))Q(t), \quad \frac{\mathrm{d}N(t)}{\mathrm{d}t} \ge -D(t)N(t),$$

for all $t \in I$. Hence,

$$Q(t) \ge Q(0)\exp\left(-\int_0^t \mu_1(u, Q(u))\mathrm{d}u\right),$$

and

$$N(t) \ge N(0)\exp\left(-\int_0^t D(u)\mathrm{d}u\right),$$

for all $t \in I$. Consequently, there are positive constants $Q_0$ and $N_0$ such that $Q(t) \ge Q_0$ and $N(t) \ge N_0$ for all $t \in I$.

Since

$$\frac{\mathrm{d}Q(t)}{\mathrm{d}t} \le \rho_1(t, S(t), Q(t)) \le \rho_1(t, S_1, Q_0),$$

for all $t \in I$, we directly obtain that there is a constant $Q_1 > 0$ such that $Q(t) \le Q_1$ for all $t \in I$. Since, further,

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} \le \mu_1(t, Q(t))N(t) \le \mu_1(t, Q_1)N(t),$$

for all $t \in I$, we obtain that $N(t)$ also is bounded on $I$, say $N(t) \leq N_1$ for all $t \in I$. By ($H_3$), we obtain further

$$\begin{aligned}\frac{\mathrm{d}S(t)}{\mathrm{d}t} &\geq -b(t)S(t) - N(t)\rho_2(t, S(t), Q(t)) \\ &\geq -b(t)S(t) - N_1\rho_2(t, S(t), 0) \\ &= -b(t)S(t) - N_1\frac{\partial\rho_2(t, \xi(t), 0)}{\partial S}S(t) \\ &\geq -k_2S(t),\end{aligned}$$

for all $t \in I$, where $\xi(t) \in (0,\ S(t))$ and

$$k_2 = \sup\left\{b(t) + N_1\frac{\partial\rho_2(t, S, 0)}{\partial S} : t \geq 0,\ 0 \leq S \leq S_1\right\}.$$

Obviously, $k_2 < \infty$. Hence, there is a constant $S_0 > 0$ such that $S(t) \geq S_0$ for all $t \in I$. From the above discussion we obtain finally

$$\inf_{t\in I}\{S(t), Q(t), N(t)\} > 0, \quad \sup_{t\in I}\{S(t), Q(t), N(t)\} < \infty,$$

which leads to a contradiction. This completes the proof. □

On the boundedness of all solutions of model (2) we have the following result.

**Theorem 2** *Suppose that* $(H_1) - (H_6)$ *hold. Then there is a constant* $M_0 > 0$ *such that any positive solution* $(N(t), S(t), Q(t))$ *of model (2)*

$$\limsup_{t\to\infty} N(t) < M_0, \quad \limsup_{t\to\infty} S(t) < M_0, \quad \limsup_{t\to\infty} Q(t) < M_0.$$

*Proof* Let $(N(t), Q(t), S(t))$ be any solution of model (2) with the initial value $(N(0), Q(0), S(0)) \in R^3_+$. From Theorem 1, we have that $(N(t), Q(t), S(t))$ is defined on $R_{+0}$ and is positive. Since

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} \leq a(t) - b(t)S(t) \quad \text{for all} \quad t \in R_{+0},$$

by the comparison principle and conclusion $(a)$ of Lemma 1 for $\alpha = 0$, we can obtain that there exists a $T_0 > 0$ such that

$$S(t) \leq S^*(t) + \gamma_0 < 2M_1 \quad \text{for all} \quad t \geq T_0,$$

where constant $\gamma_0 \in (0,\ 1)$ is given in Lemma 2. Further since

$$\frac{\mathrm{d}Q(t)}{\mathrm{d}t} \leq \rho_1(t, S^*(t) + \gamma_0, Q(t)) - \mu_2(t, Q(t))Q(t),$$

for all $t \geq T_0$, by the comparison principle and conclusion $(a)$ of Lemma 2 for $\alpha = \gamma_0$, we can obtain that there exists a $T_1 > T_0$ such that

$$Q(t) \leq Q_{\gamma_0}(t) \leq M_2 + \gamma_0 < 2M_2,$$

for all $t \geq T_1$, where $Q_{\gamma_0}(t)$ is the solution of the following equation

$$\frac{\mathrm{d}Q(t)}{\mathrm{d}t} = \rho_1(t, S^*(t) + \gamma_0, Q(t)) - \mu_2(t, Q(t))Q(t),$$

satisfying the initial condition $Q_{\gamma_0}(T_0) = Q(T_0)$.

Write $B = \max\{2M_1, 2M_2\}$. From $(H_2)$ to $(H_6)$ we can choose the positive constants $\epsilon_0, \epsilon_1, r, N_0$ and $T^*$, satisfying $\epsilon_0 < \epsilon_1 < 1$ and $\epsilon_0 < \inf_{t \in R_{+0}} S^*(t)$, such that for all $t \geq T^*$

$$\int_t^{t+\omega} (\mu_1(u, \epsilon_1 \exp(\beta\omega)) - D(u))\mathrm{d}u \leq -r,$$

$$\int_t^{t+\omega} (\frac{\rho_1(u, \epsilon_0, \epsilon_1)}{\epsilon_1} - \mu_2(u, \epsilon_1))\mathrm{d}u \leq -r,$$

and

$$a(t) - b(t) - N_0\rho_2(t, \epsilon_0, B) \leq -r, \tag{12}$$

where

$$\beta = \sup_{t \in R_{+0}} \left\{ \frac{\rho_1(t, \epsilon_0, \epsilon_1)}{\epsilon_1} + \mu_2(t, \epsilon_1) \right\}.$$

By $(H_2)$ and $(H_5)$ we have $\beta < \infty$.

We first will prove

$$\liminf_{t \to \infty} N(t) \leq N_0. \tag{13}$$

In fact, if (13) is not true, then there is $T^* \geq T_1$ such that $N(t) > N_0$ for all $t \geq T^*$. If $S(t) \geq \epsilon_0$ for all $t \geq T^*$, then by (12) we have

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} \leq a(t) - b(t)\epsilon_0 - N_0\rho_2(t, \epsilon_0, B) < -\gamma \tag{14}$$

for all $t \geq T^*$. It follows $S(t) \to -\infty$ as $t \to \infty$ which is contradiction. Hence, there is a $t_1 > T^*$ such that $S(t_1) < \epsilon_0$. Further, if there is a $t_0 > t_1$ such that $S(t_0) > \epsilon_0$, then there is a $t^* \in (t_1, t_0)$ such that $S(t^*) = \epsilon_0$, and $S(t) > \epsilon_0$ for all $t \in (t^*, t_0]$. Hence, we have $\frac{dS(t^*)}{dt} \geq 0$. However, on the other hand, in view of (12) we have

$$\frac{dS(t^*)}{dt} \leq a(t^*) - b(t^*)\epsilon_0 - N_0\rho_2(t^*, \epsilon_0, B) < 0.$$

Therefore, a contradiction is obtained. This shows $S(t) \leq \epsilon_0$ for all $t \geq t_1$.

If $Q(t) \geq \epsilon_1$ for all $t \geq t_1$, then

$$\begin{aligned}\frac{dQ(t)}{dt} &= Q(t)(\frac{\rho_1(t, S(t), Q(t))}{Q(t)} - \mu_2(t, Q(t))) \\ &\leq Q(t)(\frac{\rho_1(t, \epsilon_0, \epsilon_1)}{\epsilon_1} - \mu_2(t, \epsilon_1)),\end{aligned}$$

for all $t \geq t_1$. Consequently,

$$Q(t) \leq Q(t_1) \exp \int_{t_1}^{t} (\frac{\rho_1(t, \epsilon_0, \epsilon_1)}{\epsilon_1} - \mu_2(t, \epsilon_1))dt$$

for all $t \geq t_1$. Since

$$\int_{t_1}^{\infty} (\frac{\rho_1(t, \epsilon_0, \epsilon_1)}{\epsilon_1} - \mu_2(t, \epsilon_1))dt = -\infty,$$

we obtain $\lim_{t\to\infty} Q(t) = 0$ which leads to a contradiction. Hence, there exists a $t_2 > t_1$ such that $Q(t_2) < \epsilon_1$. If further there exists a $t_3 > t_2$ such that $Q(t_3) > \epsilon_1 \exp(\beta\omega)$, then by the continuity of $Q(t)$ there exists a $t_4 \in (t_2, t_3)$ such that $Q(t_4) = \epsilon_1$ and $Q(t) > \epsilon_1$ for all $t \in (t_4, t_3]$. Choosing an integer $p \geq 0$ such that $t_3 \in [t_4 + p\omega, t_4 + (p+1)\omega)$, then we obtain

$$\begin{aligned}\epsilon_1 \exp(\beta\omega) &< Q(t_3) \\ &= Q(t_4) \exp \int_{t_4}^{t_3} \left(\frac{\rho_1(t, S(t), Q(t))}{Q(t)} - \mu_2(t, Q(t))\right) dt \\ &\leq \epsilon_1 \exp \int_{t_4}^{t_3} \left(\frac{\rho_1(t, \epsilon_0, \epsilon_1)}{\epsilon_1} - \mu_2(t, \epsilon_1)\right) dt\end{aligned}$$

$$= \epsilon_1 \exp\left[\int\limits_{t_4}^{t_4+\omega} + \cdots + \int\limits_{t_4+(p-1)\omega}^{t_4+p\omega} + \int\limits_{t_4+p\omega}^{t_3}\right]\left(\frac{\rho_1(t,\epsilon_0,\epsilon_1)}{\epsilon_1} - \mu_2(t,\epsilon_1)\right)\mathrm{d}t$$
$$\leq \epsilon_1 \exp \int\limits_{t_4+p\omega}^{t_3}\left(\frac{\rho_1(t,\epsilon_0,\epsilon_1)}{\epsilon_1} - \mu_2(t,\epsilon_1)\right)\mathrm{d}t$$
$$\leq \epsilon_1 \exp(\beta\omega),$$

which leads to a contradiction. Hence, we finally have

$$Q(t) \leq \epsilon_1 \exp(\beta\omega) \quad \text{for all} \quad t \geq t_2. \tag{15}$$

From this, we immediately obtain

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} \leq N(t)(\mu_1(t, \epsilon_1 \exp(\beta\omega)) - D(t)),$$

for all $t \geq t_2$. Integrating from $\tau$ to $t$ it follows

$$N(t) \leq N(\tau) \exp \int\limits_{\tau}^{t} (\mu_1(v, \epsilon_1 \exp(\beta\omega)) - D(v))\mathrm{d}v.$$

By (13), we further obtain $N(t) \to 0$ as $t \to \infty$, which leads to a contradiction. Therefore, (13) is true.

Now, we prove that there is a constant $M_6 > 0$ such that

$$\limsup_{t\to\infty} N(t) \leq M_6. \tag{16}$$

If (16) is not true, then there is an initial value sequence $\{z_n = (N_n, S_n, Q_n)\} \subset R^3_+$ such that

$$\limsup_{t\to\infty} N(t, z_n) > (2N_0 + 1)n \quad \text{for all} \quad n = 1, 2, 3, \ldots.$$

In view of (13), for each $n$, there are two time sequences $\{v_q^{(n)}\}$ and $\{t_q^{(n)}\}$, satisfying $0 < v_1^{(n)} < t_1^{(n)} < v_2^{(n)} < t_2^{(n)} < \cdots < v_q^{(n)} < t_q^{(n)} < \cdots$ and $v_q^{(n)} \to \infty$ as $q \to \infty$, such that

$$N(v_q^{(n)}, z_n) = 2N_0, \quad N(t_q^{(n)}, z_n) = (2N_0 + 1)n,$$

and

$$2N_0 < N(t, z_n) < (2N_0 + 1)n \quad \text{for all} \quad t \in (v_q^{(n)}, t_q^{(n)}).$$

Obviously, there are $T^{(n)} > 0$ and $K^{(n)} > 0$ such that $S(t, z_n) < B$ and $Q(t, z_n) < B$ for all $t \geq T^{(n)}$ and $v_q^{(n)} > T^{(n)}$ for all $q \geq K^{(n)}$. Since

$$\frac{\mathrm{d}N(t, z_n)}{\mathrm{d}t} \leq N(t, z_n)(\mu_1(t, B) - D(t)) \quad \text{for all} \quad t \geq T^{(n)},$$

when $q \geq K^{(n)}$, integrating the above inequality from $v_q^{(n)}$ to $t_q^{(n)}$ we have

$$n \leq \exp \int\limits_{v_q^{(n)}}^{t_q^{(n)}} (\mu_1(v, B) - D(v))\mathrm{d}v.$$

Consequently, by assumption ($H_3$)

$$t_q^{(n)} - v_q^{(n)} \to \infty \quad \text{as} \quad n \to \infty \quad \text{and} \quad q \geq K^{(n)}. \tag{17}$$

By (11), ($H_2$) and ($H_4$)–($H_6$) we can choose a constant $P > 0$ such that for any $t \geq P$ and $a \in R_+$

$$\int\limits_a^{a+t} (\mu_1(v, \epsilon_1 \exp(\beta\omega)) - D(v))dv < -\gamma,$$

$$\int\limits_a^{a+t} (\frac{\rho_1(t, \epsilon_0, \epsilon_1)}{\epsilon_1} - \mu_2(t, \epsilon_1))dt < \ln\left(\frac{\epsilon_1}{B}\right)$$

and $\gamma P > B - \epsilon_0$. By (17), there is an $N^* > 0$ such that $t_q^{(n)} > v_q^{(n)} + 3P$ for all $n \geq N^*$ and $q \geq K^{(n)}$. For any $n \geq N^*, q \geq K^{(n)}$, if $S(t) \geq \epsilon_0$ for all $t \in [v_q^{(n)}, v_q^{(n)} + P]$, then we have

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} \leq a(t) - b(t)\epsilon_0 - N_0\rho_2(t, \epsilon_0, B) < -\gamma.$$

Consequently

$$\epsilon_0 \leq S(v_q^{(n)} + P, z_n) \leq S(v_q^{(n)}, z_n) - \gamma P < \epsilon_0,$$

which is a contradiction. Hence, there is a $t_1 \in [v_q^{(n)}, v_q^{(n)} + P]$ such that $S(t_1, z_n) < \epsilon_0$. A similar argument as in above we can prove $S(t, z_n) < \epsilon_0$ for all $t \geq t_1$.

If $Q(t, z_n) \geq \epsilon_1$ for all $t \in [t_1, t_1 + P]$, then we have

$$\frac{\mathrm{d}Q(t)}{\mathrm{d}t} \leq Q(t)\left(\frac{\rho_1(t, \epsilon_0, \epsilon_1)}{\epsilon_1} - \mu_2(t, \epsilon_1)\right)$$

for all $t \in [t_1,\ t_1 + P]$, consequently,

$$\begin{aligned} \epsilon_1 &\le Q(t_1 + P) \\ &\le Q(t_1) \exp \int_{t_1}^{t_1+P} (\frac{\rho_1(t, \epsilon_0, \epsilon_1)}{\epsilon_1} - \mu_2(t, \epsilon_1))\mathrm{d}t \\ &< B \exp\left(\ln\left(\frac{\epsilon_1}{B}\right)\right) = \epsilon_1, \end{aligned}$$

which is a contradiction. Hence there is a constant $t_2 \in [t_1,\ t_1 + P]$ such that $Q(t_2, z_n) < \epsilon_1$. A similar argument as in above we further can prove $Q(t, z_n) < \epsilon_1 \exp(\beta\omega)$ for all $t \ge t_2$. From this, we obtain

$$\frac{\mathrm{d}N(t, z_n)}{\mathrm{d}t} \le N(t, z_n)(\mu_1(t, \epsilon_1 \exp(\beta\omega)) - D(t)) \quad \text{for all} \quad t \in [t_2,\ t_q^{(n)}].$$

Therefore,

$$\begin{aligned} (2N_0 + 1)n &= N(t_q^{(n)}, z_n) \\ &\le N(\tau_0, z_n) \exp \int_{\tau_0}^{t_q^{(n)}} (\mu_1(v, \epsilon_1 \exp(\beta\omega)) - D(v))\mathrm{d}v \\ &< (2N_0 + 1)n, \end{aligned}$$

which is a contradiction. This shows that (16) is true. Choose a constant $M_0 > \max\{B, M_6\}$, then we finally have

$$\lim_{t\to\infty} \sup N(t) < M_0, \quad \lim_{t\to\infty} \sup S(t) < M_0, \quad \lim_{t\to\infty} \sup Q(t) < M_0.$$

This completes the proof. □

**Remark 2** The biological meanings of Theorems 1 and 2 are very obvious, because in a chemostat the sizes of cultured phytoplankton cells $N$, nutrients $S$ and $Q$ actually must be nonnegative and limited.

## 4 Permanence

Let $Q^*(t)$ be some fixed positive solutions of Eq. 4 with initial condition $Q^*(0) = Q_0^* > 0$. On the permanence of species $N$ of model (2) we have the following result.

**Theorem 3** *Suppose that* $(H_1)$–$(H_6)$ *hold. If there exists a constant* $\lambda > 0$ *such that*

$$\lim_{t\to\infty} \inf \lambda^{-1} \int_{t}^{t+\lambda} (\mu_1(v, Q^*(v)) - D(v))\mathrm{d}v > 0, \tag{18}$$

*then species* $N$ *of model (2) is permanent.*

*Proof* In view of conclusion ($a$) of Lemma 2 we have directly $0 < \inf_{t\geq 0} Q^*(t) \leq \sup_{t\geq 0} Q^*(t) < \infty$. We first prove that there is a constant $\alpha > 0$ such that for any positive solution $(N(t), S(t), Q(t))$ of model (2)

$$\limsup_{t\to\infty} N(t) > \alpha. \tag{19}$$

From (18), ($H_2$), ($H_4$) and ($H_6$) we can choose the positive constants $\epsilon$ and $T_1$ such that $\inf_{t\in R_{+0}} Q^*(t) - \epsilon > 0$ and

$$\int_t^{t+\lambda} (\mu_1(v, Q^*(v) - \epsilon) - D(v))\mathrm{d}v \geq \epsilon \tag{20}$$

for all $t \geq T_1$. For any small enough constant $\alpha > 0$, we consider the following two auxiliary equations

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \rho_1(t, S^*(t) - \alpha, y) - \mu_2(t, y)y, \tag{21}$$

and

$$\frac{\mathrm{d}z}{\mathrm{d}t} = a(t) - \alpha\rho_1(t, M_0, 0) - b(t)z, \tag{22}$$

where $M_0$ is given in Theorem 2. Let $y_\alpha(t)$ and $z_\alpha(t)$ be the solutions of Eqs. 21 and 22 with initial values $y_\alpha(0) = Q_0^*$ and $z_\alpha(0) = S_0^*$, respectively. By conclusion ($c$) of Lemmas 1 and 2, we obtain that $y_\alpha(t)$ converges to $Q^*(t)$ and $z_\alpha(t)$ converges to $S^*(t)$ uniformly for all $t \in R_+$ when $\alpha \to 0$. Hence, there is a constant $\alpha = \alpha(\epsilon) > 0$ with $2\alpha < \epsilon$ such that

$$y_\alpha(t) \geq Q^*(t) - \frac{\epsilon}{2}, \quad z_\alpha(t) \geq S^*(t) - \frac{\epsilon}{2} \quad \text{for all} \quad t \in R_+. \tag{23}$$

If $\limsup_{t\to\infty} N(t) < \alpha$, then from Theorem 2 there is a $T_2 \geq T_1$ such that $N(t) < \alpha$, $S(t) < M_0$ and $Q(t) < M_0$ for all $t \geq T_2$. Since

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} \geq a(t) - b(t)s(t) - \alpha\rho_2(t, M_0, 0),$$

for all $t \geq T_2$, by the comparison theorem we have $S(t) \geq z(t)$ for all $t \geq T_2$, where $z(t)$ is the solution of Eq. 22 with initial value $z(T_2) = S(T_2)$. By conclusion ($b$) of Lemma 2, $z_\alpha(t)$ is globally uniformly attractive. Hence, there is a enough large $T_3 \geq T_2$ such that

$$z(t) \geq z_\alpha(t) - \frac{\epsilon}{2} \quad \text{for all} \quad t \geq T_3.$$

By (23) we further obtain

$$z(t) \geq z_\alpha(t) - \frac{\epsilon}{2} \geq S^*(t) - \epsilon \quad \text{for all} \quad t \geq T_3. \tag{24}$$

It follows from (24), that

$$\frac{dQ(t)}{dt} \geq \rho_1(t, S^*(t) - \epsilon, Q(t)) - \mu_2(t, Q(t))Q(t).$$

By the comparison theorem we have $Q(t) \geq y(t)$ for all $t \geq T_3$, where $y(t)$ is the solution of Eq. 21 with initial value $y(T_3) = Q(T_3)$. By conclusion ($b$) of Lemma 2, $y_\alpha(t)$ is globally uniformly attractive. Hence, there is a enough large $T_4 \geq T_3$ such that

$$y(t) \geq y_\alpha(t) - \frac{\epsilon}{2} \quad \text{for all} \quad t \geq T_4.$$

Hence,

$$Q(t) \geq y_\alpha(t) - \frac{\epsilon}{2} \geq Q^*(t) - \epsilon \quad \text{for all} \quad t \geq T_4.$$

Since

$$\frac{dN(t)}{dt} \geq N(t)(\mu_1(t, Q^*(t) - \epsilon) - D(t)),$$

for all $t \geq T_4$, by integrating we have

$$N(t) \geq N(T_4) \exp\left[\int_{T_4}^{t} (\mu_1(v, Q^*(v) - \epsilon) - D(v))dv\right].$$

By (20), it follows that $N(t) \to \infty$ as $t \to \infty$, which is a contradiction. Therefore, (19) is true.

Suppose that the conclusion of Theorem 3 is not true, then there is a sequence $\{z_n = (N_n, S_n, Q_n)\} \subset R^3_{+0}$ such that

$$\liminf_{t\to\infty} N(t, z_n) < \frac{\alpha}{n+1} \quad \text{for all} \quad n = 1, 2, 3, \ldots,$$

where $2\alpha < \epsilon$. In view of (12), for each $n$, there are two time sequences $\{v_q^{(n)}\}$ and $\{t_q^{(n)}\}$, satisfying $0 < v_1^{(n)} < t_1^{(n)} < v_2^{(n)} < t_2^{(n)} < \cdots < v_q^{(n)} < t_q^{(n)} < \cdots$ and $v_q^{(n)} \to \infty$ as $q \to \infty$, such that

$$N(v_q^{(n)}, z_n) = \alpha, \quad N(t_q^{(n)}, z_n) = \frac{\alpha}{n+1},$$

and

$$\frac{\alpha}{n+1} < N(t, z_n) < \alpha \quad \text{for all} \quad t \in (v_q^{(n)}, t_q^{(n)}).$$

Since

$$\frac{\mathrm{d}N(t, z_n)}{\mathrm{d}t} \geq -D(t)N(t, z_n),$$

integrating from $v_q^{(n)}$ to $t_q^{(n)}$ we can obtain

$$\exp \int_{v_q^{(n)}}^{t_q^{(n)}} D(v)\mathrm{d}v \geq n+1.$$

Hence,

$$t_q^{(n)} - v_q^{(n)} \to \infty \quad \text{as} \quad n \to \infty, \tag{25}$$

By (20), there are positive constants $P$ and $\eta$ such that for any $t \geq P$ and $a \in R_+$,

$$\int_a^{a+t} (\mu_1(v, Q^*(v) - \epsilon) - D(v))\mathrm{d}v > \eta. \tag{26}$$

By Theorem 2, there is a $T^{(n)} > 0$ such that

$$S(t, z_n) < M_0 \quad \text{for all} \quad t \geq T^{(n)}.$$

Obviously, there is a $K^{(n)} > 0$ such that $v_q^{(n)} > T^{(n)}$ for all $q \geq K^{(n)}$. Let $z(t)$ be the solution of Eq. 22 with the initial value $z(v_q^{(n)}) = S(v_q^{(n)}, z_n)$. Since $z_\alpha(t)$ is globally uniformly attractive for Eq. 22, we obtain that there is a $T_0 > P$ and $T_0$ is independent of any $q$ and $n$ such that

$$z(t) \geq z_\alpha(t) - \frac{\epsilon}{2} \quad \text{for all} \quad t \geq T_0 + v_q^{(n)}. \tag{27}$$

Let $y(t)$ be the solution of Eq. 21 with the initial value $y(v_q^{(n)} + T_0) = Q(v_q^{(n)} + T_0, z_n)$. Since $y_\alpha(t)$ is globally uniformly attractive for Eq. 21, we obtain that there is a $T^* > P$ and $T^*$ is independent of any $q$ and $n$ such that

$$y(t) \geq y_\alpha(t) - \frac{\epsilon}{2} \quad \text{for all} \quad t \geq T^* + v_q^{(n)} + T_0.$$

By (23), there is an $N^* > 0$, such that $t_q^{(n)} > v_q^{(n)} + T_0 + T^* + P$ for all $n > N^*$ and $q \geq K^{(n)}$. For any $n$ and $q \geq k^{(n)}$, we have

$$\frac{\mathrm{d}S(t, z_n)}{\mathrm{d}t} \geq a(t) - b(t)S(t, z_n) - \alpha\rho_2(t, M_0, 0), \tag{28}$$

for all $t \in [v_q^{(n)}, t_q^{(n)}]$ By (28) and the comparison theorem, it follows $S(t, z_n) \geq z(t)$ for all $t \in [v_q^{(n)}, t_q^{(n)}]$ and $q \geq K^{(n)}$. Hence, from (24) for any $n \geq N^*$ and $q \geq K^{(n)}$ we have

$$S(t, z_n) \geq z(t) \geq S^*(t) - \epsilon \quad \text{for all} \quad t \in [v_q^{(n)} + T_0, t_q^{(n)}].$$

Further, since

$$\frac{\mathrm{d}Q(t, z_n)}{\mathrm{d}t} \geq \rho_1(t, S^*(t) - \epsilon, Q(t, z_n)) - \mu_2(t, Q(t, z_n))Q(t, z_n), \tag{29}$$

for all $t \in [v_q^{(n)} + T_0,\ t_q^{(n)}]$, by the comparison theorem, it follows that $Q(t, z_n) \geq y(t)$ for all $t \in [v_q^{(n)} + T_0,\ t_q^{(n)}]$ and $q \geq K^{(n)}$. Hence, from (23) and the above inequality, for any $n \geq N^*$ and $q \geq K^{(n)}$ we have

$$Q(t, z_n) \geq y(t) \geq Q^*(t) - \epsilon \quad \text{for all} \quad t \in [v_q^{(n)} + \tilde{T}, t_q^{(n)}],$$

where $\tilde{T} = T_0 + T^*$. Since

$$\frac{\mathrm{d}N(t, z_n)}{\mathrm{d}t} \geq N(t, z_n)(\mu_1(t, Q^*(t) - \epsilon) - D(t)),$$

for all $t \in [v_q^{(n)} + \tilde{T}, t_q^{(n)}]$, by integrating we have

$$N(t_q^{(n)}, z_n) \geq N(v_q^{(n)} + \tilde{T}, z_n) \exp \int_{v_q^{(n)}+\tilde{T}}^{t_q^{(n)}} (\mu_1(v, Q^*(v) - \epsilon) - D(v))\mathrm{d}v.$$

From this and by (25) we obtain

$$\begin{aligned} \frac{\alpha}{n+1} &\geq \frac{\alpha}{n+1} \exp \int_{v_q^{(n)}+\tilde{T}}^{t_q^{(n)}} (\mu_1(v, Q^*(v) - \epsilon) - D(v))\mathrm{d}v \\ &> \frac{\alpha}{n+1}, \end{aligned}$$

which is a contradiction. This completes the proof. □

**Remark 3** In model (2) the $\mu_1(t, Q)$ and $D(t)$ indicate the growth rate and the removal rate of the phytoplankton cells, respectively. So, $\mu_1(t, Q) - D(t)$ is the intrinsic growth rate of phytoplankton cells. On the other hand, let $(S(t), Q(t), N(t))$ be any positive solution of model (2), then one can prove that $\limsup_{t\to\infty} S(t) \le \limsup_{t\to\infty} S^*(t)$ and $\limsup_{t\to\infty} Q(t) \le \limsup_{t\to\infty} Q^*(t)$ . Hence, when time is large enough, $S^*(t)$ and $Q^*(t)$ can be take for the available maximum value of $S(t)$ and $Q(t)$, respectively. Thus, in inequality (18), $\mu_1(t, Q^*(t)) - D(t)$ is the available maximum value of phytoplankton $N$ at time $t$. The left hand of inequality (18) indicates inferior limit of the maximum intrinsic growth rate in the mean of phytoplankton $N$ on interval $[t, t + \lambda]$. Therefore, Theorem 3 shows that phytoplankton cells must be permanent when the inferior limit value is positive.

Further, on the permanence of nutrients $S$ and $Q$ for model (2), we have the following result.

**Theorem 4** *Suppose that* $(H_1)$–$(H_6)$ *hold. Let* $(N(t), S(t), Q(t))$ *be any positive solution of model (2).*

*(a) If species N is strong persistent, then nutrient S and quota Q also are strong persistent.*
*(b) If species N is permanent, then nutrient S and quota Q also are permanent.*

*Proof* We only give the proof of conclusion $(a)$. We firstly prove that if species $N$ is strongly persistent then quota $Q$ is also strongly persistent. Choose positive constants $\eta$ and $T_0$ such that

$$\int_t^{t+\omega} (\mu_1(v, \eta) - D(v))\mathrm{d}v < -\eta \quad \text{for all} \quad t \ge T_0. \tag{30}$$

If there is a $T_1 > 0$ such that $Q(t) < \eta$ for all $t \ge T_1$, then we have

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} \le N(t)(\mu_1(t, \eta) - D(t)) \quad \text{for all} \quad t \ge T_1.$$

Integrating from $T_1$ to $t$ we obtain

$$N(t) \le N(T_1) \exp \int_{T_1}^{t} (\mu_1(v, \eta) - D(v))\mathrm{d}v.$$

From this and by (30), it follows that $N(t) \to 0$ as $t \to \infty$. This leads to a contradiction with the strong persistence of $N$. Therefore, we have $\limsup_{t\to\infty} Q(t) \ge \eta$.

If $\liminf_{t\to\infty} Q(t) = 0$, then there are two time sequences $\{t_q\}$ and $\{s_q\}$, satisfying $0 < s_1 < t_1 < s_2 < t_2 < \cdots < s_q < t_q < \cdots$, such that for each $q = 1, 2, \ldots$

$$Q(t_q) = \frac{\eta}{q^2}, \quad Q(s_q) = \frac{\eta}{q},$$

and

$$\frac{\eta}{q^2} < Q(t) < \frac{\eta}{q} \quad \text{for all} \quad t \in (s_q,\ t_q).$$

Since

$$\begin{aligned}\frac{\mathrm{d}Q(t)}{\mathrm{d}t} &= \rho_1(t, S(t), Q(t)) - \mu_2(t, Q(t))Q(t)\\ &\geq -\mu_2(t, \eta)Q(t),\end{aligned}$$

for all $t \in [s_q,\ t_q]$, we have

$$\exp \int_{s_q}^{t_q} \mu_2(t, \eta)\mathrm{d}t \geq q \quad \text{for all} \quad q = 1, 2, \ldots.$$

Hence, $t_q - s_q \to \infty$ as $q \to \infty$. Let $\liminf_{t\to\infty} N(t) = \alpha > 0$ by the strong persistence of $N$ and further let $N_0 = \sup_{t\in R_{+0}} N(t)$, then $N_0 < \infty$ by Theorem 2. By (30), there is a constant $P > 0$ such that

$$N_0 \exp \int_{t}^{t+a} [\mu_1(s, \eta) - D(s)]\mathrm{d}s < \frac{\alpha}{2} \quad \text{for all} \quad t \in R_{+0},\ a \geq P.$$

Choose a $q_0 > 0$ such that $t_q - s_q \geq P$ for all $q \geq q_0$, then for any $q \geq q_0$, we have

$$N(t_q) \leq N(s_q) \exp \int_{s_q}^{t_q} (\mu_1(t, \eta) - D(t))\mathrm{d}t \leq \frac{\alpha}{2}.$$

Hence, $\liminf_{t\to\infty} N(t) \leq \liminf_{q\to\infty} N(t_q) \leq \frac{\alpha}{2} < \alpha$ which leads to a contradiction. Therefore, quota $Q$ is strongly persistent. Next, a similar argument as in above, we can prove that if quota $Q$ is strongly persistent, then nutrient $S$ is also strongly persistent. This completes the proof of conclusion $(a)$. □

**Remark 4** The biological meaning of the Theorem 4 is very obvious, because in model (1) survival of the phytoplankton cells depends only on internal stored nutrient $Q$, and internal stored nutrient $Q$ depends only on external nutrient $S$. Hence, if nutrient $S$ can not survive, then nutrient $Q$ also can not survive. Consequently, phytoplankton $N$ will extinct. Whereas, if phytoplankton cells in chemostat survive, then all nutrient both in internal and external nutrient survive.

When model (2) degenerated into the periodic case, i.e. $a(t), b(t)$ and $D(t)$ are continuous and $\omega$-periodic functions and $\rho_i(t, S, Q)$ and $\mu_i(t, Q)$ $(i=1, 2)$ are continuous and $\omega$-periodic functions with respect to $t \in R$, then we can easily obtain that solution $S^*(t)$ of system (3) and $Q^*(t)$ of system (5) are also periodic. Therefore, from Theorem 3- 4 and Theorem on existence of periodic solution in [6, Theorem 1], we have following Corollary.

**Corollary 1** *Suppose that model (2) is $\omega$-periodic and* $(H_1)$–$(H_6)$ *hold. If*

$$\int_0^{\omega} (\mu_1(v, Q^*(v)) - D(v))\mathrm{d}v > 0,$$

*then $S(t)$, $Q(t)$ and $N(t)$ are permanent, and model (2) has at least one positive $\omega$-periodic solution.*

## 5 Extinction

Lastly, on the extinction of species $N$ of model (2), we have the following result.

**Theorem 5** *Suppose that* $(H_1)$–$(H_6)$ *hold. If there is a constant* $\omega > 0$ *such that*

$$\limsup_{t\to\infty} \omega^{-1} \int_t^{t+\omega} (\mu_1(v, Q^*(v)) - D(v))\mathrm{d}v < 0, \tag{31}$$

*then for any positive solution* $(N(t), S(t), Q(t))$ *of model (2)*

$$\lim_{t\to\infty} N(t) = 0, \quad \lim_{t\to\infty} (S(t) - S^*(t)) = 0. \quad \lim_{t\to\infty} (Q(t) - Q^*(t)) = 0.$$

*Proof* By ($H_4$), we can choose a sufficient small constant $r_0 > 0$ and a large enough constant $T_0 > 0$ such that

$$\int_t^{t+\omega} (\mu_1(v, Q^*(v) + \epsilon) - D(v))\mathrm{d}v \le -r_0 \quad \text{for all} \quad \epsilon \in [0, r_0],\ t \ge T_0. \tag{32}$$

Consider the following equation

$$\frac{\mathrm{d}y(t)}{\mathrm{d}t} = \rho_1(t, S^*(t) + \alpha, y(t)) - \mu_2(t, y(t))y(t). \tag{33}$$

By conclusion $(c)$ of Lemma 2, we obtain that for any $\epsilon \in (0, r_0]$ there is a constant $\alpha_\epsilon > 0$ such that solution $y(t)$ of Eq. 33 with $\alpha = \alpha_\epsilon$ and initial condition $y(0) = Q^*(0)$ satisfies

$$y(t) \le Q^*(t) + \frac{\epsilon}{2} \quad \text{for all} \quad t \in R_{+0}.$$

Since

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} \le a(t) - b(t)S(t) \quad \text{for all} \quad t \ge 0,$$

in view of the comparison theorem and conclusion $(a)$ of Lemma 1, we obtain that for any $\alpha > 0$ there is a constant $T(\alpha) \ge T_0$ such that

$$S(t) \le S^*(t) + \alpha \quad \text{for all} \quad t \ge T(\alpha). \tag{34}$$

Particularly, we have

$$S(t) \le S^*(t) + \alpha_\epsilon \quad \text{for all} \quad t \ge T(\alpha_\epsilon). \tag{35}$$

Further, since

$$\begin{aligned}\frac{\mathrm{d}Q(t)}{\mathrm{d}t} &= \rho_1(t, S(t), Q(t)) - \mu_2(t, Q(t))Q(t) \\ &\le \rho_1(t, S^*(t) + \alpha_\epsilon, Q(t)) - \mu_2(t, Q(t))Q(t),\end{aligned}$$

for all $t \ge T(\alpha_\epsilon)$, by comparison theorem and conclusion $(b)$ of Lemma 2 there is a $T_2 \ge T(\alpha_\epsilon)$ such that

$$Q(t) \le y(t) + \frac{\epsilon}{2} \quad \text{for all} \quad t \ge T_2.$$

Therefore, we finally have

$$Q(t) \le Q^*(t) + \epsilon \quad \text{for all} \quad t \ge T_2.$$

By $(\mathrm{H}_4)$ it follows for any $t > T_2$

$$\begin{aligned}N(t) &= N(T_2)\exp\int_{T_2}^{t}(\mu_1(v, Q(v)) - D(v))\mathrm{d}v \\ &\le N(T_2)\exp\int_{T_2}^{t}(\mu_1(v, Q^*(v) + \epsilon) - D(v))\mathrm{d}v.\end{aligned}$$

Therefore, by (32) we finally have $N(t) \to 0$ as $t \to \infty$.

For any small enough $\eta > 0$, we consider the following auxiliary equation

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} = a(t) - b(t)S(t) - \eta\rho_2(t, S^*(t) + \alpha, 0). \tag{36}$$

Let $S^*_\eta(t)$ be the positive solution of system (36) with initial value $S^*_\eta(0) = S^*(0)$. By conclusion $(c)$ of Lemma 1, for any $\alpha > 0$ there is a $\eta > 0$ such that $|S^*_\eta(t) - S^*(t)| < \frac{\alpha}{2}$

for all $t \in R_{+0}$. Since $N(t) \to 0$ as $t \to \infty$, for any $\eta > 0$ there is a $T_\eta \geq T_2$ such that $N(t) < \eta$ for all $t \geq T_\eta$. Hence

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} \geq a(t) - b(t)S(t) - \eta\rho_2(t, S^*(t) + \alpha, 0) \quad \text{for all} \quad t \geq T_\eta.$$

From the comparison theorem and the global attractivity of $S^*_\eta(t)$ by conclusion (*b*) of Lemma 1, we can obtain that there is a $T_3 \geq T_\eta$ such that $S(t) > S^*_\eta(t) - \frac{\alpha}{2}$ for all $t > T_3$. Hence

$$S(t) > S^*(t) - \alpha \quad \text{for all} \quad t > T_3. \tag{37}$$

Combining with (35) we finally obtain

$$|S(t) - S^*(t)| < \alpha \quad \text{for all} \quad t > T_3.$$

This shows $S(t) \to S^*(t)$ as $t \to \infty$.

Finally, a similar argument as in above we can prove $Q(t) \to Q^*(t)$ as $t \to \infty$. This completes the proof. □

**Remark 5** The biological meaning of the Theorem 5 is also very obvious. In fact, given similar explanation as to remark 3, left hand of inequality (3.1) indicate inferior limit of maximum intrinsic growth in the mean of phytoplankton on interval $[t, t+\omega]$. Therefore, Theorem 5 shows that phytoplankton $N$ must be permanent when inferior limit of maximum intrinsic growth in the mean of phytoplankton on interval $[t, t+\omega]$ is negative.

When model (2) is periodic, as a corollary of Theorem 5, we have following result.

**Corollary 2** *Suppose that model (2) is $\omega$ periodic and $(H_1)$–$(H_6)$ hold. If*

$$\int_0^\omega (\mu_1(v, Q^*(v)) - D(v))\mathrm{d}v < 0,$$

*then for any solution $(S(t), Q(t), N(t))$ of model (2), we have $N(t) \to 0$ as $t \to \infty$.*

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