

Stability analysis for a single-species chemostat model with age structure and contribution of population to resource

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Abstract In an ecosystem some populations not only consume the resource but also contribute themselves to the resource after senescence and other deaths and considered another source of resource. In view of these facts and based on whether the population individual is capable of reproduction, a single-species chemostat model with age structure and the contribution to resource is formulated and analyzed. We introduce two thresholds \mathfrak{R}_0 and α_0 by the method of next generation matrix and further obtain conditions of stability for equilibria. Our results indicate that the population can be eradicated if the input concentration of external resource α is controlled under a threshold α_0 . In addition, the results show that the contribution of population to resource make threshold value α_0 larger, which implies, in view of the biological meaning, that such contribution plays a negative role in suppressing population.

Keywords Chemostat · Stage structure · Next generation matrix · Global stability

1 Introduction

The chemostat is an important and well-adopted laboratory apparatus used to culture microorganisms. It has been used for different systems such as lakes, wastewater treatment processes and biological reactors producing genetically altered organisms.

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Some studies of chemostat models have focused on age-structured single-species systems of microorganisms feeding on some limited resource. In a chemostat setting, Droop [1] found that a population of single-celled *Monochrysis lutheri* showed persistent oscillations at low dilution rates despite attempts to achieve a steady state. Some models of single-celled organisms feeding on an abiotic resource in a chemostat have incorporated aspects of cell life-history through the cell cycle [2,3] and have found oscillations for some parameter values, suggesting that oscillations are caused by cyclic interactions between density dependence and the changing stage or age structure of the population. McNair et al. [4] studied rotifers feeding on photosynthetic algae (in the dark, so that the algae could be considered a non-reproducing resource) and found that the rotifers displayed persistent oscillations. They tried to explain the observed oscillations using a stage-structured model. Fussmann et al. [5] incorporated simple age structure of rotifers in a rotifer-alga-nitrogen (predator-prey-resource) chemostat model and found that the model accurately predicted when persistent oscillations appeared in their experimental community. McCauley et al. [6] isolated stage-structured cycles from larger amplitude predator-prey cycles in their experiments with *Daphnia* feeding on algae. Recently, Toth [7] modeled an age-structured population feeding on an abiotic resource by combining the Gurtin-Mac-Camy approach with a standard chemostat model. Toth [8] introduced a single-species age-structured chemostat model with linear uptake of the resource by the population and periodic pulsing of the resource into the chemostat.

Even though considerably more attention has been given to single-species chemostat models with age structure, most of them ignored the contribution of population to resource after senescence and other deaths [9]. Motivated by this ideal, we present a new age-structured species-resource chemostat model amenable to a general qualitative analysis. The organization of this paper as follows. In the next section, we introduce a model and determine two threshold values by the method of the next generation matrix. In Sect. 3, the existence and local stability of the population-eradication equilibrium and interior equilibrium are investigated by means of the second additive compound matrix. In Sect. 4, the global stabilities of equilibria are discussed and brief conclusion is presented in Sect. 5.

2 Model formulation and thresholds

The model that we analyze is the age-structured species-resource chemostat system

$$\begin{cases} x' = \alpha - \beta x (y_1 + \sigma y_2) - \delta x + \gamma_1 y_1 + \gamma_2 y_2, \\ y_1' = \beta x (y_1 + \sigma y_2) - \delta y_1 - \varepsilon y_1 - \gamma_1 y_1, \\ y_2' = \varepsilon y_1 - \gamma_2 y_2 - \delta y_2, \end{cases} \quad (2.1)$$

System (2.1) describes a chemostat containing a resource with concentration $x(t)$ and a single age-structured population. The variable $y_1(t)$ is the concentration of the population in the chemostat that is not in reproductive age (we call this group nonproductive population), while $y_2(t)$ is the concentration of the population that is of reproductive age.

We make the following assumptions for our models:

- (H1) The parameter σ is nonnegative and the others are positive. Here $\sigma = 0$ represents that the reproductive age populations do not consume the resource. In particular, $\sigma = 1$ indicates that population individuals of two ages have the same uptake rates for resource. Otherwise, not.
- (H2) The parameter α is the input concentration of the resource per unit time and δ is the rate constant with which all organisms wash out of the chemostat.
- (H3) The Population not only consumes the resource but also contributes itself to resource after senescence and other deaths and considered another source of resource. The terms β and $\sigma\beta$ are the consumption rates of resource by nonreproductive and reproductive individuals, respectively. Some fractions γ_i , ($i = 1, 2$) of death populations are transformed into resource.
- (H4) Resource consumed by reproductive individuals are converted into the nonreproductive individuals.
- (H5) The parameter ε is the rate of the individuals transferring from the nonreproductive age $y_1(t)$ to the reproductive age $y_2(t)$.

For the sake of clarity, let $m = \delta + \varepsilon + \gamma_1$, $n = \delta + \gamma_2$. Then model (2.1) becomes

$$\begin{cases} x' = \alpha - \beta x (y_1 + \sigma y_2) - \delta x + \gamma_1 y_1 + \gamma_2 y_2, \\ y_1' = \beta x (y_1 + \sigma y_2) - m y_1, \\ y_2' = \varepsilon y_1 - n y_2. \end{cases} \tag{2.2}$$

It is obvious that the region $\{(x, y_1, y_2) \mid x > 0, y_1 \geq 0, y_2 \geq 0\}$ is positively invariant for model (2.2). For $y_1 > 0$ and $y_2 > 0$, adding up the three equations of (2.2), one gets

$$(x + y_1 + y_2)' = \delta \left(\frac{\alpha}{\delta} - x - y_1 - y_2 \right).$$

It follows that

$$\lim_{t \rightarrow \infty} (x + y_1 + y_2) = \frac{\alpha}{\delta}.$$

So the dynamics of system (2.2) is restricted in the positive invariant subset $\Omega \subset R_+^3$ defined by

$$\Omega = \left\{ (x, y_1, y_2) \in R_+^3 : x > 0, y_1 \geq 0, y_2 \geq 0, x + y_1 + y_2 \leq \frac{\alpha}{\delta} \right\}$$

Next, we derive the threshold of model (2.2) by the method of next generation matrix formulated in [10].

Let $z = (y_1, y_2, x)^T$. Then model (2.2) can be written as

$$z' = F(z) - V(z),$$

where

$$F(z) = \begin{pmatrix} \beta x(y_1 + \sigma y_2) \\ 0 \\ 0 \end{pmatrix},$$

$$V(z) = \begin{pmatrix} my_1 \\ \varepsilon y_1 + ny_2 \\ \alpha + \beta x(y_1 + \sigma y_2) + \delta x - \gamma_1 y_1 - \gamma_2 y_2 \end{pmatrix}.$$

It is easy to see that model (2.2) has a population-eradication equilibrium $E_0 = (\frac{\alpha}{\delta}, 0, 0)$ and the Jacobian matrices of $F(z)$ and $V(z)$ at E_0 are, respectively,

$$DF(E_0) = \begin{pmatrix} F_{2 \times 2} & 0 \\ 0 & 0 \ 0 \end{pmatrix}, \quad DV(E_0) = \begin{pmatrix} V_{2 \times 2} & 0 \\ \frac{\beta\alpha}{\delta} - \gamma_1 & \frac{\sigma\beta\alpha}{\delta} - \gamma_2 \\ 0 & 0 \end{pmatrix},$$

where

$$F_{2 \times 2} = \begin{pmatrix} \frac{\beta\alpha}{\delta} & \frac{\sigma\beta\alpha}{\delta} \\ 0 & 0 \end{pmatrix}, \quad V_{2 \times 2} = \begin{pmatrix} m & 0 \\ \varepsilon & n \end{pmatrix}.$$

Then the term FV^{-1} is the next generation matrix for model (2.2). It then follows that the spectral radius of matrix FV^{-1} is

$$\rho(FV^{-1}) = \frac{\beta\alpha(\sigma\varepsilon + n)}{\delta mn} = \frac{\beta\alpha(\sigma\varepsilon + \delta + \gamma_2)}{\delta(\delta + \gamma_2)(\delta + \varepsilon + \gamma_1)}.$$

According to Theorem 2 in [10], the threshold of model (2.2) is

$$\mathfrak{R}_0 = \frac{\beta\alpha(\sigma\varepsilon + \delta + \gamma_2)}{\delta(\delta + \gamma_2)(\delta + \varepsilon + \gamma_1)}. \quad (2.3)$$

For a well biological meaning, we obtain an equivalent threshold value from $\mathfrak{R}_0 = 1$:

$$\alpha_0 = \frac{\delta(\delta + \gamma_2)(\delta + \varepsilon + \gamma_1)}{\beta(\sigma\varepsilon + \delta + \gamma_2)}. \quad (2.4)$$

3 Local stability

In this section we focus on the existence and local stability of equilibria. Let the right-hand side of equalities in model (2.2) be zero. Then model (2.2) has a population-eradication equilibrium $E_0 = (\frac{\alpha}{\delta}, 0, 0)$ if $\mathfrak{R}_0 \leq 1$ or $\alpha \leq \alpha_0$. Otherwise, model (2.2) has a unique positive equilibrium $E^*(x^*, y_1^*, y_2^*)$, where

$$x^* = \frac{(\delta + \varepsilon + \gamma_1)(\delta + \gamma_2)}{\beta(\sigma\varepsilon + \delta + \gamma_2)} = \frac{mn}{\beta(\sigma\varepsilon + n)},$$

$$y_1^* = \frac{\alpha(\delta + \gamma_2)}{\delta(\delta + \gamma_2 + \varepsilon)} \left(1 - \frac{1}{\mathfrak{R}_0}\right), \quad y_2^* = \frac{\varepsilon}{\delta + \gamma_2} y_1^*.$$

Thus, we have established the following theorem.

Theorem 3.1 (i) If $\mathfrak{R}_0 \leq 1$ or $\alpha \leq \alpha_0$, then the population-eradication equilibrium E_0 is a unique equilibrium of model (2.2) on Ω . (ii) If $\mathfrak{R}_0 > 1$ or $\alpha > \alpha_0$, then model (2.2) has a unique positive equilibrium $E^*(x^*, y_1^*, y_2^*)$.

From Theorem 3.1, if the external resource input exceeds some threshold value.

Now we are ready to proceed to the stability of equilibria E_0 and E^* .

Theorem 3.2 (i) If $\mathfrak{R}_0 \leq 1$ or $\alpha \leq \alpha_0$, then population-eradication equilibrium E_0 is locally asymptotically stable. (ii) If $\mathfrak{R}_0 > 1$ or $\alpha > \alpha_0$, then population-eradication equilibrium E_0 is unstable and the equilibrium E^* is locally asymptotically stable.

Proof Computing the Jacobian of system (2.2) evaluated at E_0 , one gets the following matrix

$$J(E_0) = \begin{pmatrix} -\delta - \frac{\beta\alpha}{\delta} + \gamma_1 - \frac{\sigma\beta\alpha}{\delta} + \gamma_2 & & \\ 0 & \frac{\beta\alpha}{\delta} - m & \frac{\sigma\beta\alpha}{\delta} \\ 0 & \varepsilon & -n \end{pmatrix}.$$

Therefore, E_0 is locally asymptotically stable if $\mathfrak{R}_0 \leq 1$ or $\alpha \leq \alpha_0$, and unstable if $\mathfrak{R}_0 > 1$ or $\alpha > \alpha_0$.

Next, we will prove that the interior equilibria E^* is locally asymptotically stable. From $\beta(y_1^* + \sigma y_2^*) = my_1^*/x^*$, it follows that the Jacobian of system (2.2) evaluated at E^* is

$$J(E^*) = \begin{pmatrix} -\delta \frac{my_1^*}{x^*} - \beta x^* + \gamma_1 - \sigma\beta x^* + \gamma_2 & & \\ \frac{my_1^*}{x^*} & \beta x^* - m & \sigma\beta x^* \\ 0 & \varepsilon & -n \end{pmatrix}.$$

Let $\lambda_i (i = 1, 2, 3)$ be its eigenvalues with $Re\lambda_1 \leq Re\lambda_2 \leq Re\lambda_3$. From the fact that $m = \delta + \varepsilon + \gamma_1, n = \delta + \gamma_2$, and $x^* = mn/[\beta(\sigma\varepsilon + n)]$, it follows that

$$\det J(E^*) = -\frac{my_1^*}{x^*} [n(m - \gamma_1) - \varepsilon\gamma_2] < 0.$$

For $\det J(E^*) = \lambda_1\lambda_2\lambda_3 < 0$, there are two cases:

- (1) $Re\lambda_i < 0$ for $i = 1, 2, 3$;
- (2) $Re\lambda_1 < 0 \leq Re\lambda_2 \leq Re\lambda_3$.

Now we prove the case (2) is not true. It follows from $\beta x^* < m$ that $\text{tr}J(E^*) < 0$. That is $\lambda_1 + \lambda_2 + \lambda_3 < 0$, along with case (2), we have that $\text{Re}(\lambda_1 + \lambda_2) < 0$ and $\text{Re}(\lambda_1 + \lambda_3) < 0$.

The second additive compound matrix [11] of $J(E^*)$ (see the Appendix) is as follows:

$$J^{[2]}(E^*) = \begin{pmatrix} -\delta - \frac{my_1^*}{x^*} + \beta x^* - m & \sigma \beta x^* & \sigma \beta x^* - \gamma_2 \\ \varepsilon & -\delta - n - \frac{my_1^*}{x^*} & -\beta x^* + \gamma_1 \\ 0 & \frac{my_1^*}{x^*} & \beta x^* - m - n \end{pmatrix}.$$

Computing directly, it follows that

$$\det J^{[2]}(E^*) = -(m + n - \beta x^*) \left[\delta(m - \beta x^*) + (\delta + n)\left(\delta + \frac{my_1^*}{x^*}\right) \right] - \frac{my_1^*}{x^*} \left[\frac{my_1^*}{x^*}(m + n - \gamma_1) + (m - \gamma_1)(\delta + m - \beta x^*) + (\delta n + \varepsilon \gamma_2) \right],$$

where $\beta x^* = \frac{mn}{(\sigma \varepsilon + n)}$ is used. Notice that $\beta x^* < m$ and $m > \gamma_1$, then $\det J^{[2]}(E^*) < 0$. According to the property of the second additive compound matrix [11], the eigenvalues of $J^{[2]}(E^*)$ are $\lambda_i + \lambda_j$, $1 \leq i < j \leq 3$. Then $(\lambda_1 + \lambda_2)(\lambda_1 + \lambda_3)(\lambda_2 + \lambda_3) < 0$. Notice that $\text{Re}(\lambda_1 + \lambda_2) < 0$ and $\text{Re}(\lambda_1 + \lambda_3) < 0$, then $\text{Re}(\lambda_2 + \lambda_3) < 0$, which contradicts with case (2). Therefore, $\text{Re}\lambda_i < 0$ for $i = 1, 2, 3$. That is, E^* is locally asymptotically stable for $\mathfrak{R}_0 > 1$. The proof is completed. \square

4 Global stability

In this section, we first investigate the global stability of the population-eradication equilibrium E_0 of model (2.2), then consider the global stability of the interior equilibrium by two cases: $\sigma = 1$ and $\sigma \neq 1$ for model (2.2).

4.1 Global stability of the population-eradication equilibrium

Theorem 4.1 (i) If $\mathfrak{R}_0 \leq 1$, the population-eradication equilibrium E_0 is globally stable on Ω ;

(ii) If $\mathfrak{R}_0 > 1$, then the solutions of model (2.2) starting sufficiently close to E_0 in Ω move away from E_0 except that those starting on the invariant x -axis approach E_0 along this axis.

Proof Let $V = (n + \sigma \varepsilon)y_1 + \sigma my_2$. Then the derivative of V along solutions of system (2.2) is

$$V'|_{(2.2)} = [(n + \sigma \varepsilon)\beta x - mn](y_1 + \sigma y_2).$$

For $x < \alpha/\delta$, one gets $V'|_{(2.2)} \leq [(n + \sigma \varepsilon)\frac{\beta \alpha}{\delta} - mn](y_1 + \sigma y_2)$.

If $\mathfrak{R}_0 < 1$, then $V'|_{(2.2)} \leq \eta mn(\mathfrak{R}_0 - 1)V$ with $\eta = \min\{1/m, 1/(\sigma\varepsilon + n)\}$. Hence

$$V(t) \leq V(0)e^{\eta mn(\mathfrak{R}_0 - 1)t},$$

where $V(0) = (\sigma\varepsilon + n)y_1(0) + \sigma my_2(0)$. It follows from $\mathfrak{R}_0 < 1$ that $\lim_{t \rightarrow \infty} V(t) = 0$. Therefore, E_0 is globally attractive. Combined with the local stability, E_0 is globally asymptotically stable on Ω for $\mathfrak{R}_0 < 1$.

If $\mathfrak{R}_0 = 1$, i.e., $(n + \sigma\varepsilon)\frac{\beta\alpha}{\delta} = mn$, $V'|_{(2.2)} = \beta(n + \sigma\varepsilon)(x - \alpha/\delta)(y_1 + \sigma y_2) \leq 0$. Since $V'|_{(2.2)} = 0$ is equivalent to $x = \alpha/\delta$ or $y_1 + \sigma y_2 = 0$, then the maximum invariant set in $\{(x, y_1, y_2) \in \Omega : V' = 0\}$ is the singleton $\{E_0\}$. The global stability of E_0 for $\mathfrak{R}_0 = 1$ follows from LaSalle's invariance principle [12].

If $\mathfrak{R}_0 > 1$, or $(n + \sigma\varepsilon)\frac{\beta\alpha}{\delta} > mn$, there exists a positive value ϵ such that $(n + \sigma\varepsilon)\frac{\beta\alpha}{\delta} > mn + \epsilon$. Then $V'|_{(2.2)} \geq [\beta(n + \sigma\varepsilon)(x - \alpha/\delta) + \epsilon](y_1 + \sigma y_2)$. Therefore, $V'|_{(2.2)} > 0$ for $x > \frac{\alpha}{\delta} - \frac{\epsilon}{(\beta(\sigma\varepsilon + n))}$, $y_1 > 0$ and $y_2 > 0$. This implies that solutions of model (2.2) starting from the region

$$\bar{\Omega} = \left\{ (x, y_1, y_2) : x > 0, y_1 \geq 0, y_2 \geq 0, x + y_1 + y_2 \leq \frac{\alpha}{\delta}, x > \frac{\alpha}{\delta} - \frac{\epsilon}{(\beta(\sigma\varepsilon + n))} \right\}$$

move away from E_0 . The proof is completed. □

Next, we give equivalent results of Theorem 4.1 for a well biological meaning. They are given in the following corollary

Corollary 4.1 (i) *The population-eradication equilibrium E_0 is globally stable on Ω if $\alpha \leq \alpha_0$. (ii) *The solutions of mode (2.2) starting sufficiently close to E_0 in Ω move away from E_0 except that those starting on the invariant x -axis approach E_0 along this axis if $\alpha > \alpha_0$.**

4.2 Global stability of the interior equilibrium

For the convenience, substituting $x = \alpha/\delta - y_1 - y_2$ into the middle equation of model (2.2) we obtain

$$\begin{cases} y_1' = \beta(\alpha/\delta - y_1 - y_2)(y_1 + \sigma y_2) - my_1, \\ y_2' = \varepsilon y_1 - ny_2. \end{cases} \tag{4.1}$$

Obviously, the dynamical behavior of model (4.1) is the same as that of model (2.2). Then, we consider system (4.1) in the region $\text{int } \Omega' = \{(y_1, y_2) : y_1 > 0, y_2 > 0, y_1 + y_2 \leq \frac{\alpha}{\delta}\}$.

To investigate the global stability of the interior equilibrium, the following discussion consists of two cases for model (2.2): $\sigma = 1$ and $\sigma \neq 1$.

Case 1: $\sigma = 1$. In this case, model (4.1) can be rewritten as

$$\begin{cases} y_1' = \beta(\alpha/\delta - y_1 - y_2)(y_1 + y_2) - (\delta + \varepsilon + \gamma)y_1, \\ y_2' = \varepsilon y_1 - (\gamma_2 + \delta)y_2. \end{cases} \tag{4.2}$$

By change of variables:

$$u = y_1 + y_2, \quad w = \frac{y_2}{y_1 + y_2}, \quad (4.3)$$

(4.2) becomes

$$\begin{cases} u' = u[k - \beta u - (\gamma_2 - \gamma_1)w], \\ w' = \varepsilon - w[h - \beta u - (\gamma_2 - \gamma_1)w], \end{cases} \quad (4.4)$$

where $k = \beta\alpha/\delta - (\delta + \gamma_1)$, $h = \beta\alpha/\delta + \varepsilon + \gamma_1 + \gamma_2$. By (4.3), the region Ω' becomes $\bar{\Omega}' = \{(u, w) : 0 < u \leq \alpha/\delta, 0 < w < 1\}$. From Theorem 3.1, when $\Re_0 > 1$, system (4.4) has a unique positive equilibrium $\bar{E}^*(u^*, w^*)$ in $\bar{\Omega}'$, where

$$u^* = \frac{\alpha}{\delta} \left(1 - \frac{1}{\Re_0}\right), \quad w^* = \frac{\varepsilon}{\delta + \gamma_2 + \varepsilon}.$$

Further, about the global stability of \bar{E}^* for system (4.4) we have:

Theorem 4.2 *If $\Re_0 > 1$ and $\sigma = 1$, the positive equilibrium \bar{E}^* of system (4.4) in $\bar{\Omega}'$ is globally asymptotically stable.*

Proof Define functions

$$V_1 = u - u^* - u^* \ln \frac{u}{u^*} \quad \text{and} \quad V_2 = w - w^* - w^* \ln \frac{w}{w^*}.$$

Then the derivatives of V_1 and V_2 along the solution of system (4.4) are

$$V_1'|_{(4.4)} = -\beta(u - u^*)^2 - (\gamma_2 - \gamma_1)(u - u^*)(w - w^*)$$

and

$$\begin{aligned} V_2'|_{(4.4)} &= \frac{w - w^*}{w} [\varepsilon - w(h - \beta u - (\gamma_2 - \gamma_1)w)] \\ &= \frac{w - w^*}{w} [w^*(h - \beta u^* - (\gamma_2 - \gamma_1)w^*) - w(h - \beta u - (\gamma_2 - \gamma_1)w)] \\ &= \frac{w - w^*}{w} [(w - w^*)(h - \beta u^* - (\gamma_2 - \gamma_1)w^*) + w(\beta(u - u^*) + (\gamma_2 - \gamma_1)(w - w^*))] \end{aligned}$$

Since $h - \beta u^* - (\gamma_2 - \gamma_1)w^* = \varepsilon/w^* = \delta + \gamma_2 + \varepsilon$ and $w < 1$, then

$$\begin{aligned} V_2'|_{(4.4)} &= -(w - w^*)^2 \left(\frac{\delta + \gamma_2 + \varepsilon}{w}\right) + \beta(u - u^*)(w - w^*) \\ &\leq -(\delta + \gamma_2 + \varepsilon)(w - w^*)^2 + \beta(u - u^*)(w - w^*). \end{aligned}$$

Define a function by $V = \theta V_1 + V_2$, where θ is a positive constant satisfying

$$(\gamma_1 - \gamma_2)^2 \theta^2 - 2\theta\beta[\gamma_1 + \gamma_2 + 2(\delta + \varepsilon)] + \beta^2 < 0. \tag{4.5}$$

It is easy to verify the existence of value θ for (4.5). Next, taking the derivative of function V with respect to time along the solutions of system (4.4), one gets that

$$V'|_{(4.4)} \leq -\beta\theta(u - u^*)^2 - [\theta(\gamma_2 - \gamma_1) - \beta](u - u^*)(w - w^*) - (\delta + \gamma_1 + \varepsilon)(w - w^*)^2.$$

By (4.5), one gets that $V'|_{(4.4)} \leq 0$, and that $V'|_{(4.4)} = 0$ if and only if $u = u^*$, $w = w^*$. Therefore, according to the Lyapunov asymptotic stability theorem [13], the positive equilibrium \bar{E}^* of system (4.4) in $\bar{\Omega}'$ is globally asymptotically stable. The proof is completed. \square

Corollary 4.2 *If $\alpha > \alpha_0$ and $\sigma = 1$, the positive equilibrium \bar{E}^* of system (4.4) in $\bar{\Omega}'$ is globally asymptotically stable.*

Case 2 $\sigma \neq 1$. By change of variables:

$$u = \alpha/\delta - y_1 - y_2, \quad w = y_1 - \sigma y_2,$$

model (4.1) becomes

$$\begin{cases} u' = \left(\delta + \frac{\sigma\gamma_1 - \gamma_2}{\sigma - 1} \right) (\alpha/\delta - u) - \beta u w + \frac{\gamma_2 - \gamma_1}{\sigma - 1} w =: P(u, w), \\ w' = \beta u w + \sigma(\alpha/\delta - u) \left(\varepsilon + \frac{\gamma_2 - \gamma_1}{\sigma - 1} \right) + \left(\frac{\gamma_1 - \sigma\gamma_2}{\sigma - 1} - \varepsilon - \delta \right) \\ w =: Q(u, w). \end{cases} \tag{4.6}$$

Correspondingly, the region Ω_1 becomes $\hat{\Omega}$ surrounded by the lines $u = 0$, $u + w = \alpha/\delta$ and $w = \sigma(\alpha/\delta - u)$ in the $u - w$ plane. When $\Re_0 > 1$, corresponding to the interior equilibrium E^* , system (4.6) has a unique positive equilibrium $\hat{E}^*(u^*, w^*)$ in $\hat{\Omega}$, where

$$u^* = \frac{\alpha}{\delta\Re_0}, \quad w^* = \frac{\alpha}{\delta} \frac{\sigma\varepsilon + \delta + \gamma_2}{\delta + \gamma_2 + \varepsilon} \left(1 - \frac{1}{\Re_0} \right).$$

Since $\sigma \neq 1$ implies that $w + \sigma u - \frac{\sigma\alpha}{\delta} = (1 - \sigma)y_1 \neq 0$ in $\hat{\Omega}$, then we can take Dulac function as $B = (w + \sigma u - \frac{\sigma\alpha}{\delta})^{-1}$. Thus

$$\begin{aligned} \frac{\partial(BP)}{\partial u} + \frac{\partial(BQ)}{\partial w} &= \left(w + \sigma u - \frac{\sigma\alpha}{\delta} \right)^{-2} \left[(\delta + \gamma_2 + \beta w) \left(\frac{\sigma\alpha}{\delta} - \sigma u - w \right) \right. \\ &\quad \left. + \beta\sigma u \left(u + w - \frac{\alpha}{\delta} \right) \right]. \end{aligned}$$

Notice that $\frac{\sigma\alpha}{\delta} - \sigma u - w = (\sigma - 1)y_1$ and that $u + w - \frac{\alpha}{\delta} = (\sigma - 1)y_2$. Then

$$\frac{\partial(BP)}{\partial u} + \frac{\partial(BQ)}{\partial w} = (\sigma - 1) \left(w + \sigma u - \frac{\sigma\alpha}{\delta} \right)^{-2} [(\delta + \gamma_2 + \beta w) y_1 + \beta\sigma u y_2].$$

This shows that the sign of $\frac{\partial(BP)}{\partial u} + \frac{\partial(BQ)}{\partial w}$ is the same as that of $\sigma - 1$. Therefore, the system has no periodic orbits if $\mathfrak{R}_0 > 1$ and $\sigma \neq 1$. By Theorem 3.2, \hat{E}^* is locally asymptotically stable. Then we have the following result on the global stability of \hat{E}^* .

Theorem 4.3 *If $\mathfrak{R}_0 > 1$ and $\sigma \neq 1$, the positive equilibrium \hat{E}^* of system (4.6) is globally asymptotically stable in $\text{int } \hat{\Omega}$. Summarizing Theorems 4.2 and 4.3 we have:*

Theorem 4.4 *The interior equilibrium E^* of model (4.4) is globally asymptotically stable in Ω if $\mathfrak{R}_0 > 1$.*

Corollary 4.3 *The interior equilibrium E^* of model (4.4) is globally asymptotically stable in Ω if $\alpha > \alpha_0$.*

Remark 4.1 From Corollary 4.1, the population can be eradicated if the input concentration of external resource α is controlled under a threshold α_0 .

Remark 4.2 By (2.4), it is clear that the contribution of population to resource make threshold value α_0 larger. So in view of the biological meaning, this contribution plays a negative role in suppressing population.

Next, we present some numerical simulations to illustrate our conclusions. Consider the following choice of parametric values:

$$\beta = 1, \sigma = 0.4, \delta = 0.5, \gamma_1 = 0.1, \gamma_2 = 0.1, \varepsilon = 0.1, \alpha = 0.2.$$

It is easy to verify that $\alpha_0 = 0.328$ and the condition of Corollary 4.1 are satisfied. Hence the population-eradication equilibrium E_0 is globally stable. System (2.1) is numerically solved for the above choice of parameters and time series are drawn in Fig. 1a. Let $\alpha = 1.2$ and the other parameters be the same as Fig. 1a. Then the condition of Corollary 4.3 are satisfied. Hence the interior equilibrium E^* is globally stable (see Fig. 1b). Choose $\alpha = 2(1 + \sin t)$, that is limiting resource is pumped into the chemostat periodically, the population tends to oscillate periodically (see Fig. 2).

5 Conclusion

In this study, a single-species chemostat model with age structure and the contribution to resource is formulated and analyzed. By the method of next generation matrix, we introduce two thresholds \mathfrak{R}_0 and α_0 , and further obtain that the population-eradication equilibrium is globally stable if $\mathfrak{R}_0 < 1$, and the interior equilibrium is globally stable if $\mathfrak{R}_0 > 1$. Our results imply that the population can be eradicated if the input concentration of external resource α is controlled under a threshold α_0 . Furthermore,

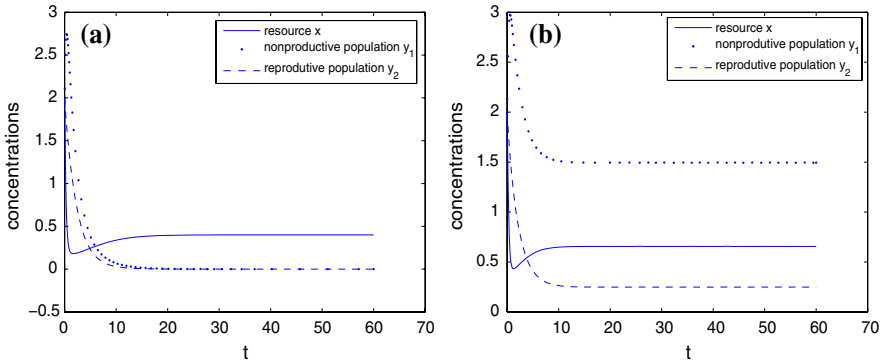


Fig. 1 a The stability of population-eradication equilibrium E_0 . b The stability of interior equilibrium E^*

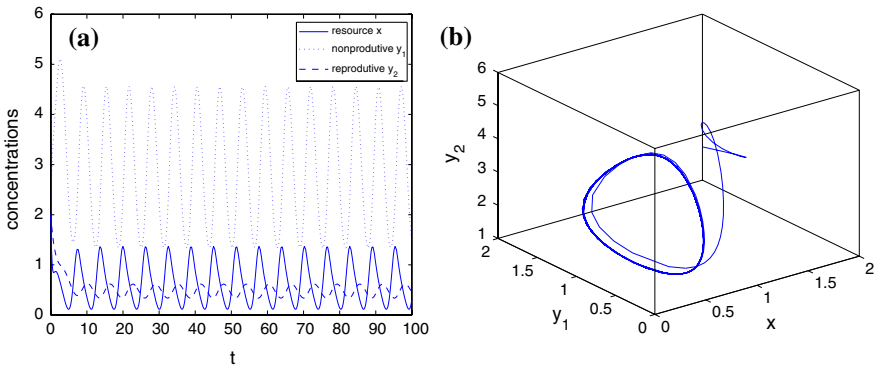


Fig. 2 Periodic solution. a Time series. b Phase portrait

it is clear that the contribution of population to resource make threshold value α_0 larger. So in view of the biological meaning, this contribution plays a negative role in suppressing population.

Appendix:the second additive compound matrix

Let $A = (a_{ij})$ be a 3×3 matrix. Then its second additive compound matrix is as follows:

$$A^{[2]} = \begin{pmatrix} a_{11} + a_{22} & a_{23} & -a_{13} \\ a_{32} & a_{11} + a_{33} & a_{12} \\ a_{31} & a_{21} & a_{22} + a_{33} \end{pmatrix}.$$

Proposition 1 Let $\sigma A = \{\lambda_i : i = 1, 2, 3\}$ be the spectrum of A . Then the spectrum of $A^{[2]}$ is $\sigma A^{[2]} = \{\lambda_i + \lambda_j : 1 \leq i < j \leq 3\}$.

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References

1. M. Droop, Vitamin B12 and marine ecology. III. An experiment with a chemostat. *J. Mar. Biol. Assoc. U.K.* **46**, 659 (1966)
2. M. Pascual, H. Caswell, From the cell cycle to population cycles in phytoplankton–nutrient interactions. *Ecology* **78**, 897 (1997)
3. I. Minkevich, A. Abramychev, The dynamics of continuous microbial culture by cell age distribution and concentration of one substrate. *Bull. Math. Biol.* **56**, 837 (1994)
4. J. McNair, M. Boraas, D. Seale, Size-structure dynamics of the rotifer chemostat: a simple physiologically structured model. *Hydrobiologia* **469**, 387–388 (1998)
5. G. Fussmann, S. Ellner, K. Shertzer, N. Hairston, Crossing the Hopf bifurcation in a live predator-prey system. *Science* **290**, 1358 (2000)
6. E. McCauley, R. Nisbet, W. Murdoch, A. DeRoos, W. Gurney, Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments. *Nature* **402**, 653 (1999)
7. D. Toth, M. Kot, Limit cycles in a chemostat model for a single species with age structure. *Math. Biosci.* **202**, 194–217 (2006)
8. D. Toth, Strong resonance and chaos in a single-species chemostat model with periodic pulsing of resource. *Chaos Solitons Fractals* **38**, 55–69 (2008)
9. D. Kalyan, R. Santanu, Effect of delay on nutrient cycling in phytoplankton–zooplankton interactions in estuarine system. *Ecol. Modell.* **215**, 69–76 (2008)
10. P. van den Driessche, J. Watmough, Reproduction numbers and sub-threshold endemic equilibria for compartmental models of disease transmission. *Math. Biosci.* **180**, 29–48 (2002)
11. M.Y. Li, J.R. Graef, L. Wang, J. Karsai, Global dynamics of a SEIR model with varying total population size. *Math. Biosci.* **160**, 191–213 (1999)
12. J.P. LaSalle, in *The Stability of Dynamical Systems*. Regional Conference Series in Applied Mathematics (SIAM, Philadelphia, PA, 1976)
13. A.M. Lyapunov, *The General Problem of the Stability of Motion* (Taylor & Francis, London, 1992)